

THE HEAD OF  
*DIPTERUS VALENCIENNESI*

Sedgwick & Murchison



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*Pp.* 1-45 ; 3 *Plates* ; 51 *Text-figures*

BULLETIN OF  
THE BRITISH MUSEUM (NATURAL HISTORY)  
GEOLOGY

Vol. 11 No. 1

LONDON: 1965

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in 1949, is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

*Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.*

*In 1965 a separate supplementary series of larger papers was instituted, numbered serially for each Department.*

*This paper is Vol. II, No. I of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

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TRUSTEES OF  
THE BRITISH MUSEUM (NATURAL HISTORY)

*Issued 9th July, 1965*

*Price Twenty-five Shillings*

# THE HEAD OF *DIPTERUS VALENCIENNESI*

Sedgwick & Murchison

By ERROL IVOR WHITE

## SYNOPSIS

There is only one known species of *Dipterus* from the Middle Old Red Sandstone of Scotland, *D. valenciennesi* Sedgwick & Murchison. The split between the dipnoan and crossopterygian stocks took place at the mosaic stage of evolution of the skull-roof bones, and the nomenclature of the consequent roofing-plates in one group has no relevance to that in the other; entirely independent systems must be used. A modified version of Forster-Cooper's alphabetical system is accepted for the dipnoans, the pattern being developed by invasion and loss rather than by fusion. There has been a gradual loss of rows of plates at the back of the dipnoan head with consequent movement forward of the occipital cross-commissure. The details of the neurocranium are described.

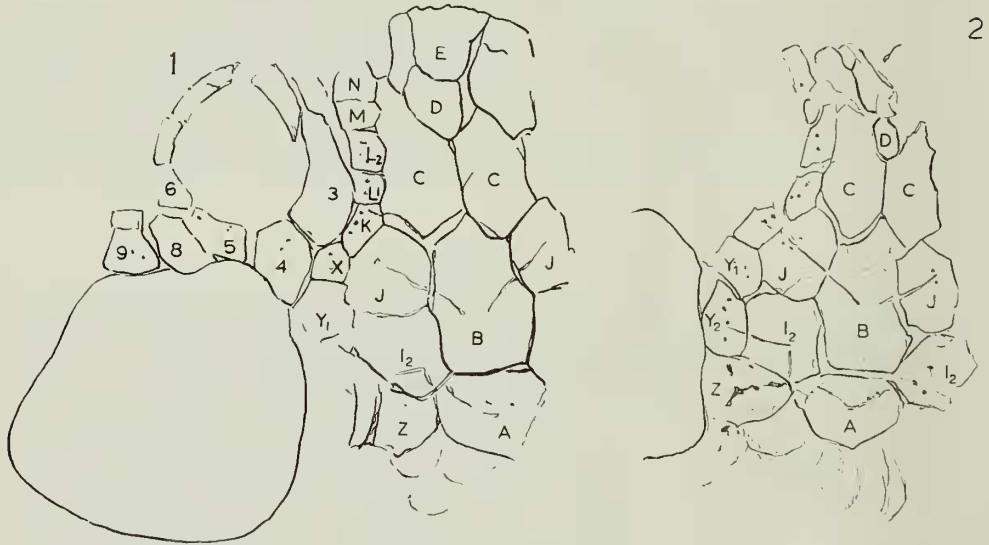
## *The Name*

SPECIMENS of *Dipterus* from the Middle Old Red Sandstone of Scotland have generally been referred to a single species, *Dipterus valenciennesi* Sedgwick & Murchison, although from time to time attempts have been made (e.g. Pander 1858 : 7 ; Watson & Day 1916 : 29) to separate the solid-snouted forms under Agassiz's (1844 : 29) specific name of *platycephalus*. More recently Westoll (1949 : 127-128) decided that the Banniskirk specimens showed sufficient peculiarities in the skull-roof pattern to warrant their separation as a distinct species, and in the belief that all Sedgwick & Murchison's (1829 : 143, pl. 15, figs. 1-3, pl. 16, figs. 1, 3, pl. 17, figs. 1-3) original specimens of their three species, *D. brachypterygius*, *D. macropygius* and *D. valenciennesi* came from Banniskirk quarry, has used the first of these names, *D. brachypterygius*, for the Banniskirk form which he considered distinct, dropping the names *D. macropygius* and *D. valenciennesi* altogether as synonyms of *D. brachypterygius*, and has revived Agassiz's name of *platycephalus* for all the other Scotch specimens of *Dipterus*, with or without solid snouts.

Unfortunately the provenance of all Sedgwick & Murchison's figured material, now in the collection of the Geological Survey, is not so certain. Only one of the specimens, a co-type of *Dipterus macropygius* (pl. 15, fig. 2 ; G.S. no. 6448) was originally labelled "Banniskirk", all the others being labelled "Thurso". "Thurso" indeed was used in early days to cover Banniskirk, which is some 8 miles to the south-east of the town, but it also covered many other quarries in the neighbourhood, and identification of the locality must depend on the recognition of matrix, a very doubtful procedure in these variable rocks. Sedgwick & Murchison's remark about "those from Banniskirk" (1829 : 142) refers to the "small number (sent to Cuvier) of the whole series afterwards examined by Messrs. Valenciennes and Pentland" (p. 142, footnote), and indeed on the previous page Sedgwick & Murchison are at pains to point out that "when the attention of geologists was first drawn to these ichthyolites, it was not known that specimens of them were to be found in any other

quarry than that of Banniskirk. The authors of this memoir have however, since discovered that similar remains are extensively . . . spread over the Caithness deposit, etc. etc. . . ." This refers to Old Red fishes in general, but clearly puts to question the origin of the specimens they figured, which are from the " more perfect remains " sent to Valenciennes & Pentland.

But even more important is the lack of substance in the supposition that the Banniskirk forms have a special pattern of their head plates, qualifying them for specific recognition. None of Sedgwick & Murchison's figured specimens shows the head-pattern clearly, and so are irrelevant to this point, whether they come from Banniskirk or not. All the five specimens from Banniskirk figured by Westoll (1949 :



FIGS. 1, 2. *Dipterus valenciennesi* S. & M. Skull-roof showing normal pattern. Banniskirk, Caithness. Fig. 1, Geol. Surv. No. 6464. Fig. 2, R.S.M. 1859.33.623 (Hugh Miller Coll.). Both  $\times 3$ .

137-139, text-fig. 4) show to some degree *brachypygopteris* features, that is, the paired bones C are replaced by the forward extension of B, and to a small extent by the medial growth of some of the lateral series K-M, although he notes that it is possible that something very like the Achanarras type ("*D. platycephalus*") occurs very rarely at Banniskirk.

One such individual was figured by Pander (1858, pl. 1, fig. 2), and his diagram (pl. 3, fig. 1) is essentially " normal " in pattern (Text-fig. 10). Of the six specimens available to me that bear *original* Banniskirk labels and show the roof pattern clearly, four (G.S. 6464, R.S.M. 1859.33.623, and R.S.M. 1876.18.31; Text-figs. 1-3) and R.S.M. 1859.33.626<sup>1</sup> show the typical normal pattern with 2 " C " plates

<sup>1</sup> The initials R.S.M. indicate that the specimen came from the Royal Scottish Museum; D.M.S.W. from Professor Watson's collection; G.S. from the Geological Survey; and M.M. from Manchester Museum. Other specimens numbered with or without an initial P, are in the British Museum (Natural History).



and a median "D", as does a fifth (33149I, Text-fig. 4) whose supposed provenance from Banniskirk has been subsequently added in pencil, presumably on the basis of the matrix. None of these five specimens would have called for comment in regard to its skull-roof.

However, on a slab recently collected at Banniskirk by Mr. Jack Saxon is a small nearly complete fish whose head certainly does call for comment, but for another reason (P. 46762D, Text-fig. 8). Two C's, a D and 2 E's are well developed in the normal way, but the hinder part of the skull is completely asymmetrical with no J on the left side, its space being largely occupied by B much swollen in front, but with some help from L<sub>1</sub> and K, on to which the rather unusual anterior pit-line extends to meet the supraorbital sensory canal. There is no indication of fusion here whatever, and indeed it is most likely that this arrangement is due to the invasion by B, and to a lesser extent by L<sub>1</sub> and K, of the area where J has failed to develop, in accordance with the sensible principle laid down by Parrington (1950: 537-540) that fusion should not be postulated unless clearly indicated.

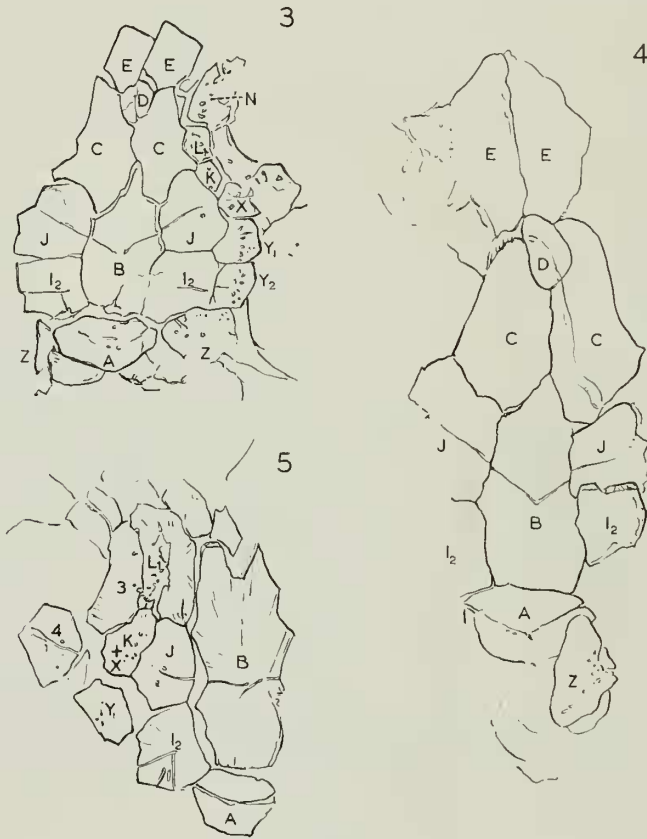
Only two of the six specimens with original Banniskirk labels show the "brachypterygopterus" pattern with the greatly enlarged plate B and no C's (42480, R.S.M. 1859.33.624, Text-figs. 5, 6), and both these specimens seem to indicate by the structure of plate B, which in each shows radiation from a single centre, that in these specimens also we have instances of plates (B) invading areas where the growth of the normal plates has been inhibited. But that it was not always entirely a matter of simple invasion is shown by one of Peach's specimens, a small skull-roof collected in 1858 at Sandside, some 10 miles west of Thurso. In this (R.S.M. 1887.35, Text-fig. 7) B is much enlarged forwards and the L bones, two on the left and one on the right side, are wide; but between their anterior ends are two very small C plates, partly fused together and partly fused to B. The front part of the skull, well separated by a *post mortem* displacement from the hinder part, shows a small M on the left, a larger M on the right, large N's on both sides, a wide single E incompletely separated from the snout, and behind this a wide plate which is evidently compound. Whether this last represents D<sup>+</sup> is not very important, but the definite natural break behind the well-defined posterior border does seem to establish that it was not part of C.

A reasonable and simple explanation of the form of the B and C and L bones in this specimen is provided by Parrington's (1956: 395-404) "Patterns of dermal bones": the development of the C bones has been retarded and much of their space occupied by B and the L bones before its growth began, and when it did make progress growth-pressure to the rear induced partial fusion with B and lateral pressure induced fusion between the two C's. That neither C bone tended to fuse with its lateral neighbour L, is noteworthy, for Westoll (1949: 135) has already remarked on the reluctance of "general" bones to fuse with "lateral line bones", and figured only two possible examples of this (1949: text-figs. 2B, 3E).

The "brachypterygopterus" pattern is not a specific character but an occasional variation, not uncommon at Banniskirk but occurring infrequently elsewhere, as at Achanarras (Parrington 1950: 540, text-figs. 4, 5). Most of the specimens showing this pattern are small, but not all, witness Parrington's second specimen.

So far as present knowledge goes one is dealing with a single variable species, and for this all three of Sedgwick & Murchison's specific names of 1828 are available (the

fourth name *macrolepidotus* refers to an osteolepid, *Thursius*—see Woodward 1891 : 373) ; but Agassiz's *platycephalus* of 1844 is not (Text-fig. 8). And Agassiz (1835 : 115) having used the inadmissible name "*macrolepidotus*", Pander (1858 : 6) as the first acceptable reviser, had the right to select whichever of the three available names that he wished for the specific name (Article 24, Internat. Code Zool. Nomenclature, XV



FIGS. 3-5. *Dipterus valenciennesi* S. & M. Fig. 3, Skull-roof showing normal pattern. Banniskirk, Caithness. R.S.M. 1876.18.31.  $\times 3$ . Fig. 4, Skull-roof showing normal pattern. ?Banniskirk. 33149(I).  $\times 3$ . Fig. 5, Skull-roof showing "brachypygopterus" pattern. Banniskirk. 42480 (Peach Coll.).  $\times 2.25$ .

Internat. Congr. Zool. 1961) : and his choice of "*valenciennesi*" was fully supported by Woodward (1891 : 236). So the name of the species remains *Dipterus valenciennesi* Sedgwick & Murchison. The term "brachypygopterus-type" may be used for the form of *D. valenciennesi* described by Westoll from Banniskirk, but from any locality, in the way that *platycephalus*-type has been used for the solid-snouted forms. In regard to this last form the original head-shield, the lectotype, upon which Agassiz based his "*Polyphractus platycephalus*" is unusually wide and small, for the numerous resorption lines and large openings of the foramina seem to indicate

an aged fish (P. 3373a, Text-fig. 51). Its small adult size, a little over 4 cm. in length, is rather unusual in the "platycephalus-type". Forster-Cooper (1937: 231) noticed a general correlation between size and the development of the snout, and it seems true that while the hard snout can occur occasionally in rather small specimens, such as this and the original of Text-fig. 7, it is invariably present in large specimens. This does not support Marshall's (1962: 314) remark that the difference between the soft and hard snouted forms "may be explained as seasonal differences": they seem more likely to be linked with size and age.

It is difficult to give absolute measurements of breadth and length in these skulls, but in general the larger skulls tend to be relatively narrower, up to about 15%, and while the smaller specimens, those measuring under 6.0 cm. from the back of B to the tip of the hard snout, have only 2 or 3 plates along the sensory canal series as a rule, *i.e.* Y<sub>2</sub>-N, not all the larger specimens show multiplication. But there are obvious exceptions to both these tendencies.

#### *Nomenclature of the Bones of the Skull-roof*

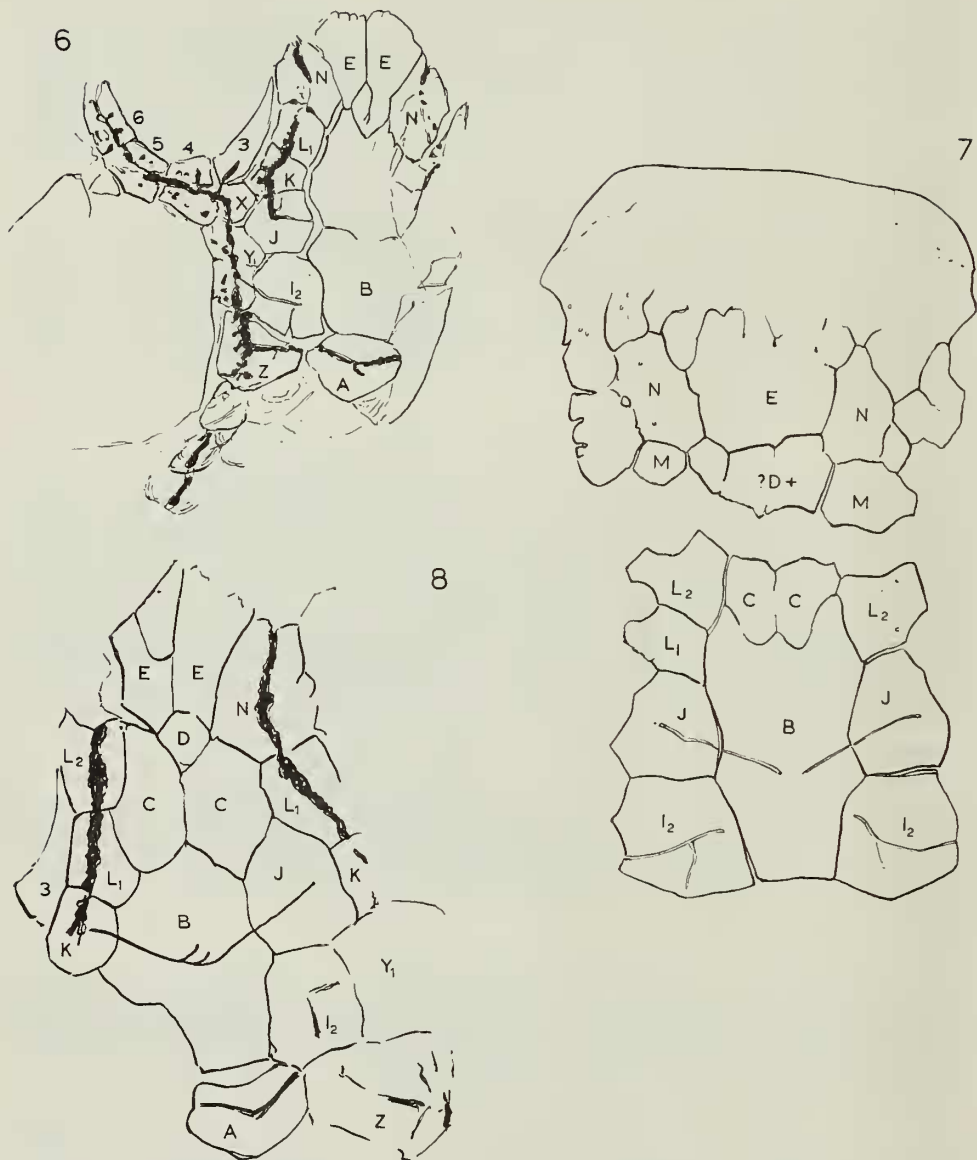
From the first the identification of the dermal bones of the skull-roof in lung-fishes gave rise to much difficulty, in the fossil forms because they had too many plates for exact correlation with those of the general run of fishes, and in the living because they had too few; and usually the earlier zoologists, such as Günther (1871), Huxley (1876) and Bridge (1898) wisely treated them with caution. The first serious attempt to identify the plates of the head of the fossil forms according to the nomenclature in general use for vertebrates was made by D. M. S. Watson (Watson & Day 1916: 29-32; Watson & Gill 1923), but his interpretation met with flat contradiction from Goodrich (1930: 305).

Since then efforts to bring order into the labelling of dipnoan roofing bones has developed along two very divergent lines: one a purely arbitrary alphabetical notation, proposed by Forster-Cooper (1936): and the other the compound nomenclature of Holmgren & Stensiö (1936), which seems in effect a more or less spatial use of the general vertebrate terms based on the assumption of widespread fusion of plates.

In a recent study of the skull-roof of a dipterine from Belgium (White 1962) the alphabetical notation of Forster-Cooper (1937: 228-229) was used without conviction or enthusiasm, merely because the alternatives seemed even less desirable. Romer's (1936: 242, text-fig. 9) code-system, if more logical in intention, is, as Westoll (1949: 126) has pointed out, incorrect in application.

On the other hand Lehman's (1959: 6) advocacy of Holmgren & Stensiö's (1936: 365, text-figs. 280 A-C) terminology, based on the theory of widespread fusion, is only acceptable if the homologies of the component bones are generally agreed, which they certainly are not.

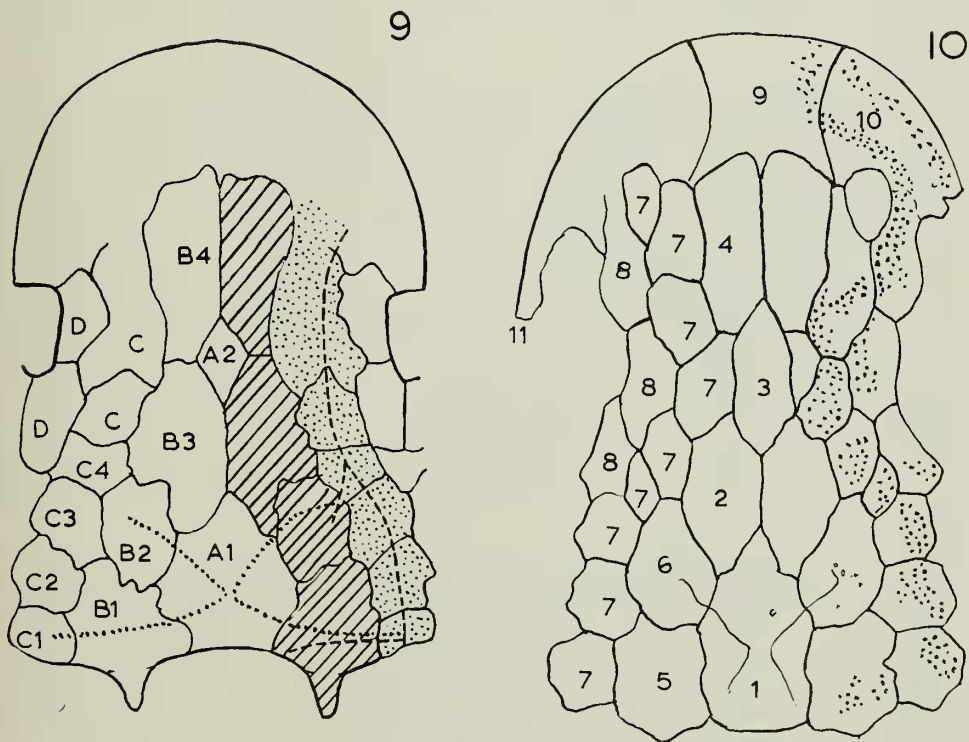
Jarvik (1948: 81, 291), while strongly supporting the fusionists, does admit that complex bones in different groups of fishes given the same name, rarely, if ever, are strictly homologous, "even in closely allied groups". He further remarks (p. 83) that "It is true that dermal bones are variable in shape and sometimes may invade the territories of adjoining bones. Thus it seems likely that the individual variations in



FIGS. 6-8. *Dipterus valenciennesi* S. & M. Fig. 6, Skull-roof, with left cheek, showing "brachypygopterus" pattern. Banniskirk, Caithness. R.S.M. 1859.33.624 (Hugh Miller Coll.).  $\times 3$ . Fig. 7, Skull-roof showing pattern intermediate between normal and "brachypygopterus" types. Sandside, Caithness. R.S.M. 1887.35 (Peach Coll.).  $\times 3$ . Fig. 8, Skull-roof of very small fish showing extremely asymmetrical hinder end. Banniskirk. P.46762D (Coll. J. Saxon, 1964).  $\times 3.5$ .

shape and extent of the dermal bones of the cranial roof in *Osteolepiformes* . . . are not always to be explained by various fusions, etc.", which comes quite near to Westoll's (1944 : 114) assertion that "the compound form (of nomenclature) . . . expresses no more than geographical extent . . .", and certainly weakens the argument for too rigid adherence to the hypothesis of universal fusion without unduly encouraging those who pin their faith overmuch on the apparently contradictory idea of "loss and invasion"—"*aut Caesar aut nihil*" may be a good political precept but it is usually a poor biological principle—indeed, Truth in Nature has a habit of falling between two schools of thought.

In spite of what has been said by their proponents concerning the advantages of either philosophy for establishing the identity or homologies of bones or their supposed components in Dipnoi, it is in practice often very difficult to identify bones by any system satisfactorily, and important mistakes and many doubtful identifications have been made on both sides. Not the smallest source of error has been due to attempts to establish the course of the canals by the openings of the tubuli on the surface of the bones; and this in the nature of things is often inevitable, since it is not always desirable or possible to dissect out the canals.



FIGS. 9, 10. Diagrams of skull-roof of *Dipterus*. Fig. 9, Diagram showing Romer's (1936 : 243, text-fig. 1c) alphabetical notation. Fig. 10, Pander's diagram of the skull-roof (1858 : 55, pl. 3, fig. 1).



*Forster-Cooper's alphabetical notation (FCAN)*

Forster-Cooper's (1937 : 228, text-fig. 3) alphabetical notation (FCAN) was based on a very simple plan, but unfortunately he never developed it fully, and sometimes used it incorrectly (e.g. pl. 7, figs. 13, 14).

It should be noted that this scheme was quite arbitrary and not based on the sensory canals and pit-lines : indeed, it is quite plain that Forster-Cooper had no clear idea of their true course. In almost every specimen that he figured and labelled he relied on the external openings of the tubuli of the sensory canals to determine their position, and sometimes mistook damaged tubercles of the ornament and *post mortem* cracks for pores and pit-lines (1937 : 233, pl. 5, fig. 9, text-fig. 5).

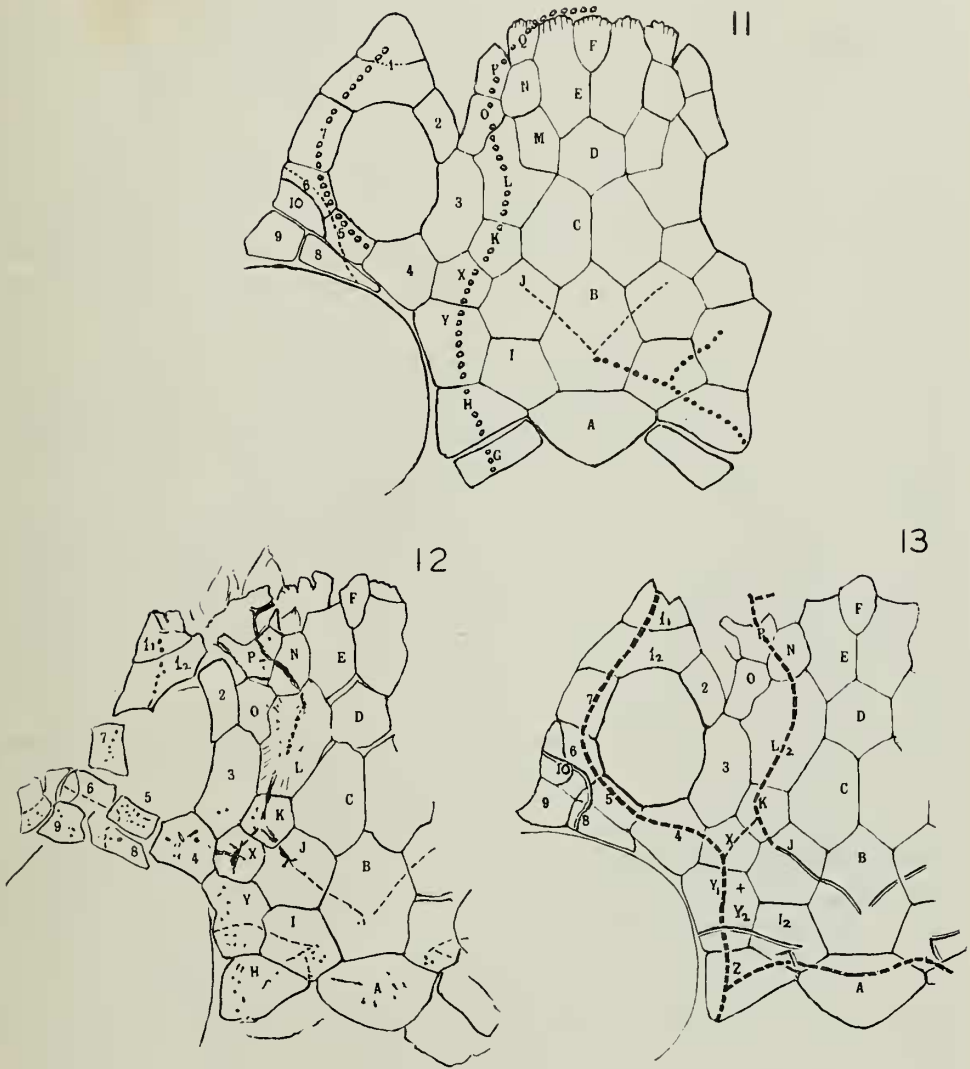
His description of the lateral lines is indeed most puzzling : " The course of the main lateral line from the body on to the head appears to run across the supra-cleithrum to the bone H. It then runs to I, where it branches, one branch going through Y, the other to B, where it meets its fellow of the opposite side. This junction is more noticeable in the *platycephalus* condition than in that of *valenciennesi*. Just in front of this point there is a V-shaped pit line pointing forwards whose arms run through the paired J bones from each side ".

In the next paragraph he stated that " The pores marking the underlying sense-organ canals always occur on the same series of bones in a line running from G through H, Y, X, K, L, O, P, Q, and then round the front of the snout at the anterior edges of E and F ".

Not only are these two statements contradictory, but both are wrong. For convenience they have been translated on to Forster-Cooper's original diagram (Text-fig. 11), the first statement shown by solid dots on the right side, the second by hollow dots on the left. Neither is supported by any of his own touched-up photographic illustrations, including that of his standard specimen (Forster-Cooper 1937 : 228, pl. 4, fig. 7, text-fig. 3) on which his diagram was based.

Apparently these statements were based on Goodrich's (1925 : 83, text-figs. 1, 3, 4) descriptions and figures, which do place the occipital commissure across Goodrich's " tabular " (H), " Post-parietal " (I) and " dermal supraoccipital " (B) just behind the anterior pit-lines, with some indication in *Dipterus* of a forward branch in the " post-parietal ", while the " supra-temporal " and " supraorbital " canals run in a continuous sinuous curve very much as Forster-Cooper describes. It may be noted that the much earlier diagram of that very acute observer C. M. Pander (1858 : 55, pl. 3, fig. 1), is a perfectly accurate representation of the skull-roof of *Dipterus* and its sensory canals (Text-fig. 10).

The general course of the canals and pit-lines is now well known, thanks to the work of Graham-Smith & Westoll (1937 : 244, text-fig. 2a), Westoll (1949 : 126, text-figs. 2, 3 etc.) and Parrington (1950 : 536, text-fig. 1). In the first paper Graham-Smith & Westoll partly rationalized Forster-Cooper's notation, using a rather better preserved head, P. 22189 from Achanarras, as the standard specimen ; plate G, which in Forster-Cooper's specimen (see Text-figs. 11, 12, 21) was a body-scale unconnected with the lateral line, was dropped; Y was allotted to two plates, and so was L on the right side as the normal pattern, the single plate on the left being considered the result of fusion. For no apparent reason Q was substituted for P. However, Westoll's remarks (1949 : 130-134) that " All these latero-sensory canal bones are



FIGS. 11-13. *Dipterus valenciennesi* S. & M. Fig. 11, Forster-Cooper's "Generalized diagram" (1937: 228, text-fig. 3) with the sensory canals and pits added from his description (p. 233), the solid dots on the right side show "the course of the main lateral line"; the rings on the left, the occurrence of the "pores marking the underlying sense-organ canals." Fig. 12, Sketch of the specimen on which Fig. 11 was based showing the distribution of the pores of the sensory canals (and of the canals themselves on the partly dissected plates X, J, K, L, N, P) and of the pit-lines. Achanarras, Caithness. P.22187.  $\times 2.3$ . Fig. 13, Corrected diagram of the same specimen with emended lettering.



extremely constant in their development, with the exception . . . that adjacent members 'fuse' ", and " There is never any difficulty in deciding where 'fusion' has occurred at least in the skull-roof " seems to the present writer to be very optimistic. Indeed Westoll's figures (1949, text-figs. 2, 3 etc.), like the earlier figures of Stensiö, are diagrammatic sketches, and the supposed source of the sensory canals was similarly based on the external pores.

Lack of more precise information doubtless accounts for Westoll's (1949 : 136) remark that " these canals show no abnormalities in the specimens studied ".

Dissections have been carried out in a number of specimens, including both Forster-Cooper's and Graham Smith & Westoll's standard specimens with interesting results.

In Forster-Cooper's specimen (*P.* 22187) part of the left side of the head has been prepared (Text-fig. 12) and the pattern is shown in diagrammatic form (Text-fig. 13). In the latter it will be noted that there is some alteration of the original lettering. G, which has already been noted as a scale, is omitted ; H, since it belongs to the main sensory canal series with Y and X, is changed to Z. But of much more significance is the absence of L<sub>1</sub> and M and the labelling of Y as Y<sub>1</sub> + Y<sub>2</sub>.<sup>1</sup> Here we are brought up against the main problem of fusion and/or replacement.

Westoll (1949 : 126, 128) although keenly critical of the fusionist tendencies of Stensiö and his school in relation to large bones, nevertheless stated that " Ontogenetical studies on living bony fishes such as *Amia* show that true fusion of adjacent bone rudiments developed along a latero-sensory canal is a normal feature of the development of large bones. It is here accepted that fusion of this type occurs in *Dipterus* " and gives (1949 : 132) some 45 instances where fusion of lateral-line elements are supposed to have occurred.

Positive detection of such fusion in more or less adult fossil skulls would presumably depend on how rudimentary the bone-rudiments were at the time of fusion : complete fusion of the earliest stages would not probably be traceable, and whether it took place or not must depend on other indirect evidence, if any.

Parrington (1950 : 545), in the second of his three important and refreshingly sane papers relating to the development of skull-bones, comments upon these supposed fusions along the lateral line series and suggests that " fusion is a result of dermal bones meeting at a time when their growth-rates exceed that of the surrounding tissues by a certain amount. The earlier appearance of neuromast rudiments would increase their chances of growing to contact other neuromast rudiments and this would increase at least the possibility of fusion ". Parrington goes on to quote the possible correlation between the increasing tendency of lateral-line elements to " fuse " with decrease in length of skull, but notes the outstanding exception, in reverse, of the long headed *Fleurantia*, where " fusion " is still marked. Later he emphasized the possibility of " almost complete capture of vacated territory " (1956) 406).

In the author's opinion Parrington's most important contributions to the questions concerning the growth and form of bones and their relationships to the sensory canals are these (Parrington 1949 : 69, 76 ; 1956 : 405, 408 etc.), which may be called " Parrington's axioms ".

<sup>1</sup> Y<sub>1</sub> and Y<sub>2</sub> are reversed from Westoll's notation so as to be in logical sequence, and I is labelled I<sub>2</sub> for reasons stated on p. 26.

1. " . . . it is unwise to assume bone fusions without the evidence of multiple centres of radiation of either the ornament or the bone structure ".

2. " . . . precursors of the dermal bones attract the growing primordia of the lateral line system and that changes in the number and positions of the dermal bones can therefore cause changes in the relations of the lateral line canals ".

Examination of the partly dissected heads here figured does seem to show that if these two principles are accepted a reasonable interpretation can be made of the bones and canals, and further for this purpose Forster-Cooper's alphabetical system of identification of the bones, as now modified, is infinitely preferable to attempts to name the bones, especially as it will be shown that the fusions postulated are only too frequently not substantiated.

### *The Sensory Canals and Pit-lines*

Before proceeding with the question of invasion or fusion of the dermal roof-bones it is necessary to confirm the course of the sensory canals of the pit-lines.

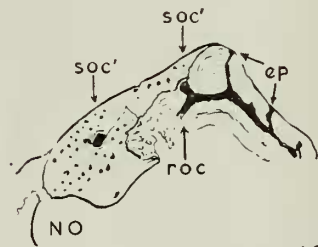
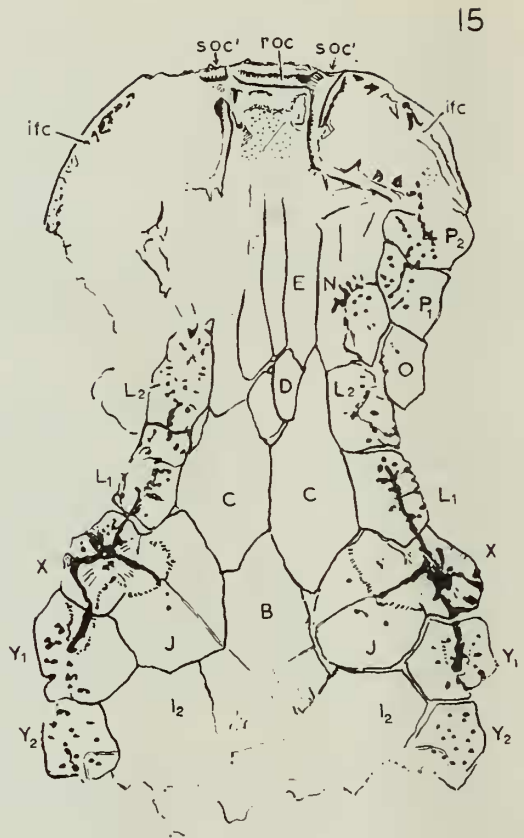
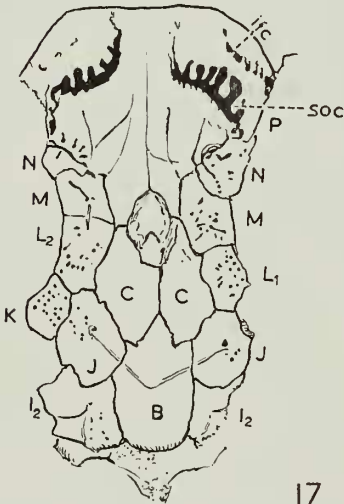
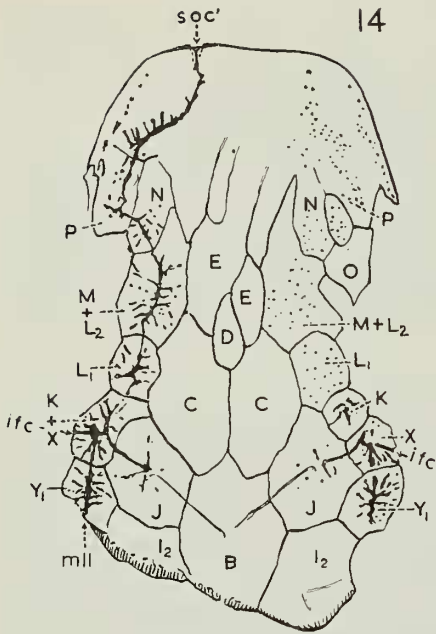
The pit-lines do vary, especially the middle and posterior lines in old specimens, but it is a variation in detail and seldom approaches the more aberrant patterns shown by Forster-Cooper's (1937 : 233, text-fig. 5). The anterior line runs forwards diagonally from B to J, and the two sides may meet in the middle or have small loops.

The middle line runs transversely from  $I_2$  into  $Y_2$  and the posterior backwards from  $I_2$  to Z. They may be in contact in  $I_2$  and have terminal twists and curls, rarely partial duplication. A well marked additional line is shown in Text-fig. 42 (P. 17410).

The general distribution of the sensory canals, as already noted, is well known, but not in any detail, especially in the snout region. The course of the supraorbital with many of the canaliculi is shown in no. 33165 (Text-fig. 14), in which the canal of the left side has been fully developed.

The supraorbital canal runs normally from the end of the anterior pit-line in J to K, and so forwards through the usual series labelled  $L_1$ ,  $L_2$  and M to N where it turns outwards to P. This plate is often incompletely separated in front from the snout. Thence the canal continues forwards, curving inwards and then again forwards and so downwards to the opening on the upper lip. This opening is so large in some specimens of *Rhinodipterus* (see White 1962 : 4, pl. 2, text-fig. 3) that Gross (1956 : 23, pl. 5, fig. 5, text-fig. 14C) identified it as the anterior nasal opening, and Ørvig (1961 : 15, pl. 3, fig. 3, text-figs. 8B, C, 9C-E) as " probably openings for glands of some sort ".

The canals of the extreme rostral region are still better demonstrated in Text-fig. 15 (P. 6087), in which the rostral commissure has been naturally weathered out, in P. 34547 and in a broken section in 33166 (Text-fig. 16). In another weathered but much flattened snout (P. 34546, Text-fig. 17) the supraorbital canal, as it turns inwards in P, apparently gives off forwards six or seven pouch-like cavities instead of the usual rounded tubuli, and such " pouches " are also indicated in P. 34558. This is almost certainly the effect of crushing and weathering, accentuated by resorption of the bone in the immediate neighbourhood of the tubuli. An intermediate stage is shown in Text-fig. 19 (P. 46690), which also shows the presence of smaller openings on the hinder side of the canal.



FIGS. 14-17. *Dipterus valenciennesi* S. & M. Fig. 14, Skull-roof in which the sensory canals have been wholly dissected out on the left side, partly on the right. Thurso, Caithness. 33165.  $\times 1.3$ . *mill*, main lateral line. For other lettering see Fig. 15. Fig. 15, Skull-roof in which the sensory canals of the snout have been naturally weathered out and some of the remainder dissected out. "Caithness". P.6087.  $\times 2$ . *ifc*, infraorbital canal. *roc*, rostral commissure. *soc'*, anterior aperture of the supraorbital canal. Fig. 16, Median part of upper lip showing both external apertures of the supraorbital canal (*soc'*), with part of rostral commissure (*roc*) and supraorbital canal itself and branches leading to external pores (*ep*) exposed by a natural longitudinal fracture. Thurso, Caithness. 33166.  $\times 2$ . Fig. 17, Skull-roof with part of canals on snout naturally weathered out. Foreshore, Clardon Haven, Caithness. P.34546. (Coll'd. D. L. Dineley, 1957).  $\times 1.3$ . *ifc*, infraorbital canal. *soc*, supraorbital canal.

The main canal runs through Z, in which it gives off the occipital commissure, first to the hinder end of  $I_2$  and then through A. From Z the main canal normally passes through  $Y_2$  and  $Y_1$ , to X, in which it turns down to pass through circumorbital 4 to form the infraorbital canal, at the same time sending a short branch to K to anastomose with the supraorbital canal.

The infraorbital canal runs through the circumorbital plates 5, 6, 7,  $I_2$ ,  $I_1$  up on to the snout, crossing the antero-lateral corners, as may be seen in most hard-snouted specimens. It may finish in a pore under the snout like the supraorbital canal, but if so the pore is often very small, and not always to be distinguished easily from the others present in this region; for the whole canal under pressure tends very readily to dissolve in the system of pores and spaces which permeate the bone there.

To give a general impression of the canal-system, the details from Text-figs. 14, 15 etc. have been superimposed on the left side of the outline of a well known, more complete skull of "platycephalus" type (P.7834, Text-fig. 18) to which plates Z-A-Z have been added and, in fig. A (P.6507), the upper lip of another specimen. The skull-roof has been figured by three other authors (Jarvik 1950, text-fig. 6; Gross 1956, text-fig. 13B; Ørvig 1961, text-fig. 7B), each giving a somewhat different interpretation of the plates, and all different from that given here. The right side shows the actual distribution of the pores in this specimen.

From this general pattern there are a number of significant deviations, as there are from the standard patterns of the head-plates, and since they are interdependent, sensory canals and head-plates will be considered together, in the light of Parrington's axioms (p. 11 *supra*) and of his theory of "Patterns of dermal bones" (1956).

It is in the lateral line series, Z-X and K-P that most difficulties arise, but there are four plates and areas that have sufficiently constant features to make them readily recognizable, Z and  $Y_1$  at the back of the skull-roof and N and P near the front.

Z, formerly H, is the hindmost plate and always roughly triangular. It receives the main-line canal from the supracleithrum and passes it on to  $Y_2$  after the canal has been joined by the occipital commissure. Only once in the series available is it in any way abnormal.

$Y_1$  always occupies the same position, just overlapping the front of the operculum, and so having a characteristic projecting angulation on the outer side. On the mesial side it lies alongside the hinder part of J and a small part of  $I_2$ . Very rarely is it replaced by, or fused with, X (Text-fig. 25; Westoll 1949, text-fig. 2B).

N is the plate, often fused with the snout, where the supraorbital canal turns outwards at the start of the sigmoid curve in front, and P (Westoll's "Q") is the plate or area in which the canal turns forward again.

A survey of the available material will make clear the advantage of a purely alphabetical system of bone nomenclature.

The first specimen to be considered must obviously be Forster-Cooper's standard specimen (P.22187, Text-figs. 11-13). Fig. 12 shows the actual specimen as it now is, partly dissected. It also shows the original lettering except that G and M are omitted, G because it was only a scale and M because its supposed presence was due to a crack in L.



The sensory canals are perfectly orthodox, as may be seen in the revised diagram (Text-fig. 13), but the series of lateral line bones show two interesting deviations, apart from the absence of M. A single bone occupies the space not only of M but of both the "L" bones and there is clearly only a single centre of growth, which from its central position is judged to be that of the middle bone of the three,  $L_2$ . There is

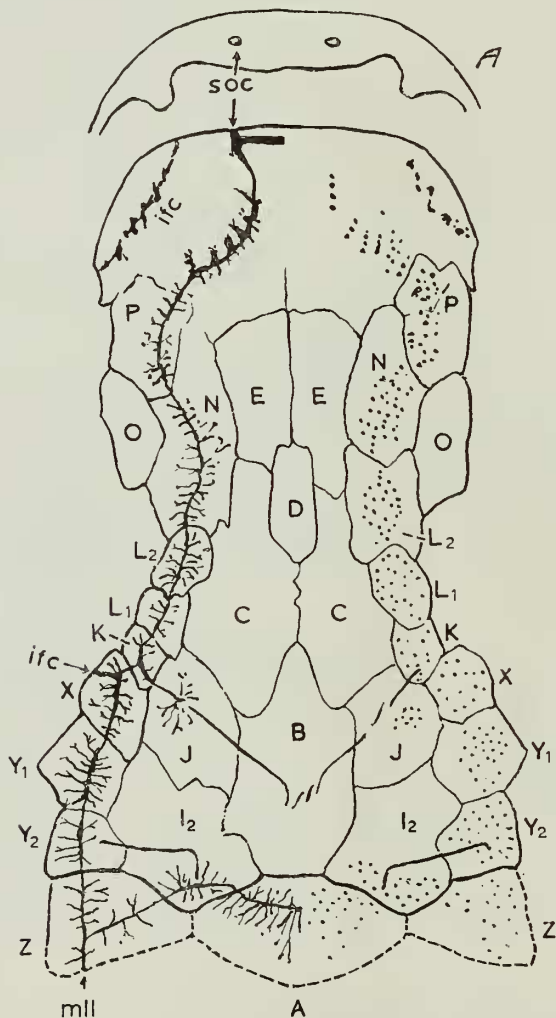


FIG. 18. *Dipterus valenciennesi* S. & M. Skull-roof of large head with plates Z-A-Z added, showing external pores of sensory canals on right side, and restoration of the canals on the left side, based on Figs. 14, 15. (cf. Jarvik 1950, text-fig. 6; Gross 1956, text-fig. 13B; Ørvig 1961, text-fig. 7B). Coast near Thurso, Caithness. P.7834.  $\times 1.5$ . A, underside of snout of similar specimen. Toldale Quarry, between Thurso and Reay, Caithness. P.6507.  $\times 1.5$ . ifc, infraorbital canal. mll, main lateral line. soc, supraorbital canal and aperture.

also only a single Y bone, but this is judged to be compound,  $Y_1 + Y_2$ , by reason of its shape and the distribution of the pores which seem to indicate two centres.

In 33165 (Text-fig. 14) the two sides make a most interesting contrast. On the wholly dissected left side a large single bone in the M-L<sub>2</sub> area does seem to have had two centres and is accordingly labelled as a compound bone, and the large odd-shaped bone between L<sub>1</sub> and Y<sub>1</sub>, is almost certainly a compound K + X. On the partly dissected right side the L<sub>1</sub> to M region is similar to the left, but the K and X area is very different, for K is not only small but is excluded from contact with C by an extension of L<sub>1</sub> and has lost to X the beginning of the supraorbital canal where it passes out of J. This is most unusual, but the result can be simply explained à la Parrington, by delay in the development of K's rudiment, which has allowed the capture of the beginning of the supraorbital canal by X and the invasion of this territory on the other side by L<sub>1</sub>.

P. 6087 (Text-fig. 15) shows the suppression of M on both sides, in favour of N on the right, and probably of L<sub>2</sub> on the left.

On both sides the important K-X region is occupied by a single, not very large bone, with a single growth centre but containing both the turn-down of the main canal at the beginning of the infraorbital canal, typical of X, and the continuation of the supraorbital canal from J, typical of K. It is not clear which has been suppressed, but it is probably K, for L<sub>1</sub> on both sides is much larger than usual and extends further backwards into the K area to meet J, as it also does on the right side in the previous figure.

In a short-headed specimen (P. 34546, Text-fig. 17) two bones only occupy the M-L position, each with a single centre and those of the left side are only superficially separated. It is probable from their forward position that the anterior bone on each side represents M, but that the hinder bone on the left side, judging by the position of the growth-centre, seems to be L<sub>2</sub>, whereas on the right L<sub>1</sub> is the more probable survivor, particularly as M is unusually large, as if it had partly replaced L<sub>2</sub>.

The fine narrow head from near Thurso (P. 7834, Text-fig. 18, p. 13 *supra*) is undissected, the sensory canals on the left side being diagrammatic. It is one of the longest heads examined, 6.9 cm. from the hinder margin of B to the tip of the snout, being only two millimetres or so shorter than the Toldale head (P. 6507, Forster-Cooper 1937, pl. 7, fig. 14) and a specimen from Edinburgh (1859.33.622), but 8 mm. less than the record head in that Museum (1901.153.2) which measures 7.7 cm. The head in Text-fig. 18 shows quite markedly contradictory tendencies, a tendency to the decrease in size of plates in the middle lateral regions (K, L<sub>1</sub>, L<sub>2</sub>) especially on the left side; but in front there is a very obvious increase in size through the suppression of M, to the advantage of N only on the left side, but also for the benefit of L<sub>2</sub> on the right. A marked difference in development of the sensory canal plates of the two sides is illustrated by a Clardon Haven specimen (P. 46690, Text-fig. 19).

Of considerable interest in showing the relationship between the distribution of pores and the actual course of the canals is the specimen (P. 22189) on which Westoll (Graham-Smith & Westoll 1937: 244, text-fig. 2a; Westoll 1943: 89, text-fig. 7c; 1949: 126, text-fig. 1) based his modified scheme of lettering.

In the original somewhat diagrammatic and restored drawings X and K are shown as a compound plate. The supraorbital canal entered this plate from J on its pos-

terior-inner side, and almost opposite this the main canal is supposed to have come in from the anterior Y plate and then turn down into circumorbital "4" to form the infraorbital canal. In fact dissection (Text-fig. 20) shows that the main canal never reaches the "X and K" bone but turns down in  $Y_1$  ( $Y_2$  of Westoll), and that the connection between the main and supraorbital canals is not only drawn out but apparently double. Examination of the structure of this supposedly compound plate shows clearly enough that it had a single growth-centre; X has failed to

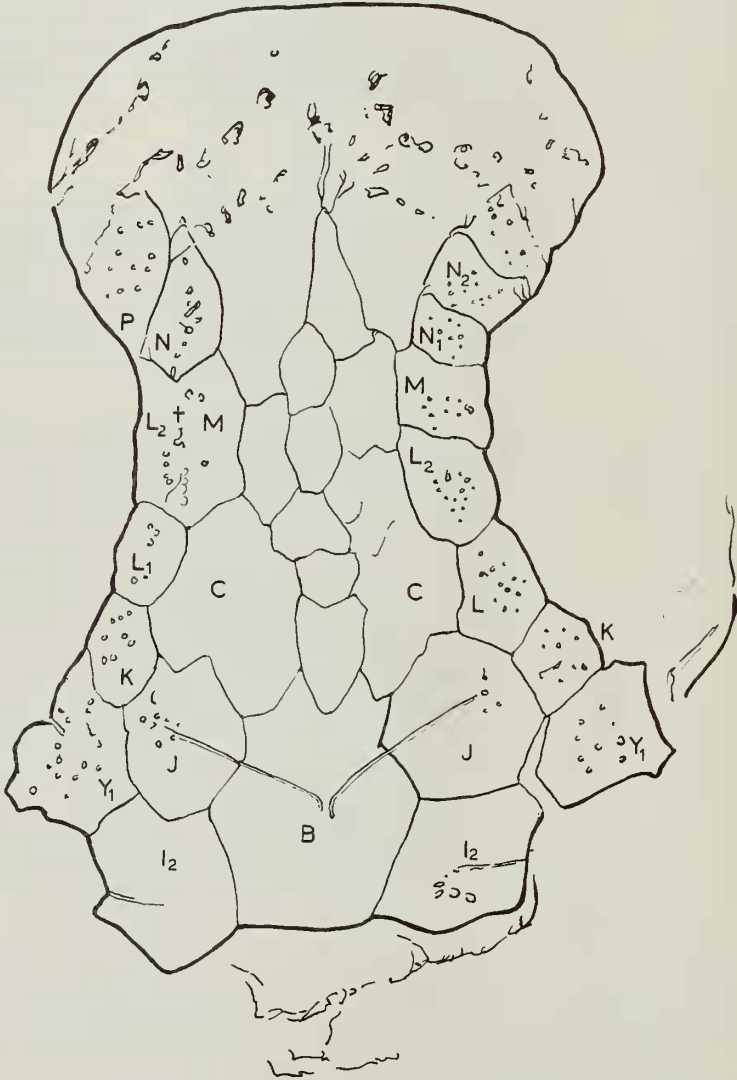


FIG. 19. *Dipterus valenciennesi* S. & M. Skull-roof showing asymmetrical development of lateral line plates. Clardon Haven, Caithness. P. 46690 (Colld. R. V. Collier, 1964).  $\times 2.25$ .



develop and its space has been largely taken by K, but the lateral line has been largely captured by  $Y_1$ . The L plate is also shown as a compound  $L_1 + L_2$ , but this has a single centre and seems to be composed of  $L_1$  only which has taken over the territory of a missing  $L_2$ .

The pores in the very small head illustrated in Text-fig. 41 (P.22194) seem to indicate a similar situation in regard to the XK area, and here also the area of M has apparently been taken over by  $L_2$ .

The capture of the infraorbital curve by  $Y_1$ , is even more clearly demonstrated in Text-fig. 21 in a very abnormal short-headed fossil from Achanarras (P.17642, cf.

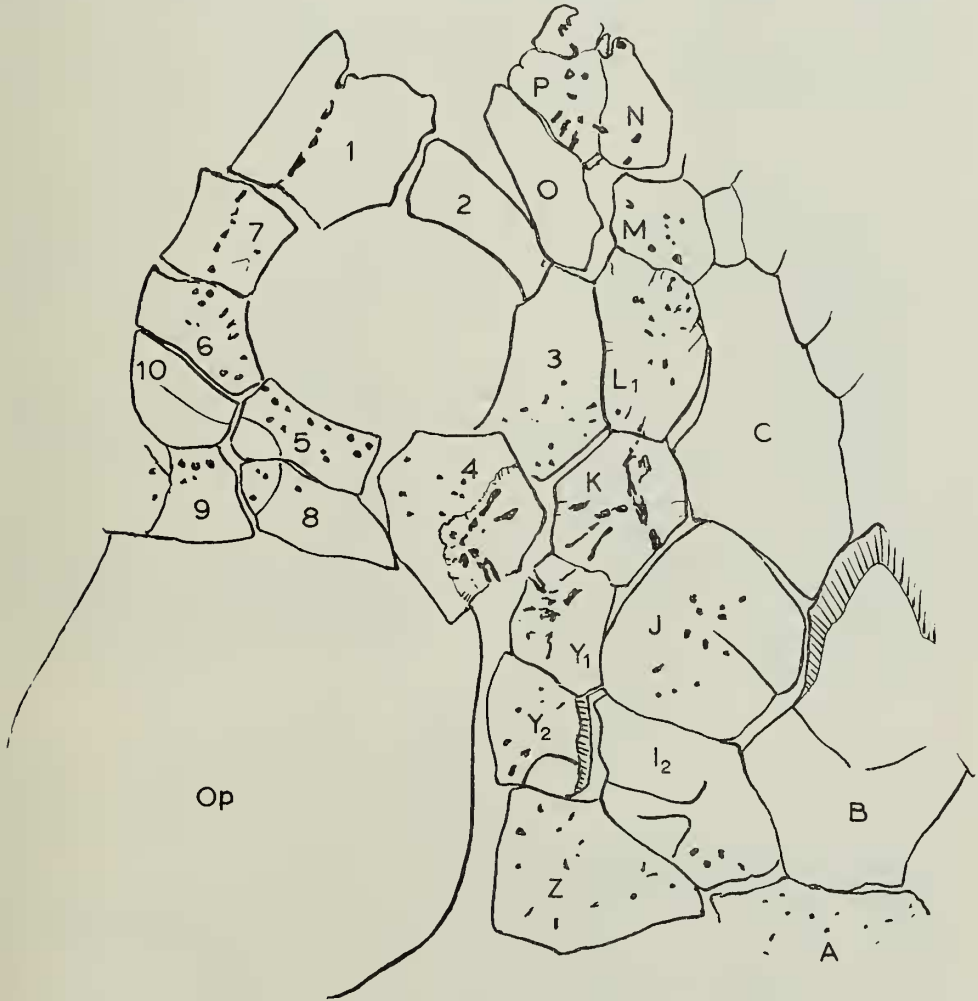


FIG. 20. *Dipterus valenciennesi* S. & M. Left side of skull-roof and cheek of original of Westoll's standard specimen (see Graham-Smith & Westoll 1937: 244, text-fig. 2a; Westoll 1949: 126, text-figs. 1A, C) with sensory canals partly dissected out and plates partly re-lettered. Achanarras, Caithness. P.22189.  $\times 3.5$ .

Forster-Cooper 1937, pl. 5, fig. 9). Plate X apparently did not develop, to judge from single-centred K, but there seems to have been some opposition by K to the annexation of the main canal by  $Y_1$ , judging by its subdivision. This fragmentation of canals owing to disturbance by fusion or elimination of plates is probably not unusual (Text-figs. 22-24). In 42403 (Text-fig. 22), a much resorbed specimen from near Wick, K and X do seem to have fused to show what appear to be double centres of growth, but nevertheless the start of the infraorbital canal has gone to  $Y_1$ .

In Text-fig. 21 another most interesting abnormality is illustrated. The supra-occipital commissure shows much disturbance owing to the non-appearance of  $Y_2$ , but instead of its space being occupied by  $Y_1$ , that bone is of the average size, and Z has grown forwards taking with it the outer end of the commissure, which crosses  $I_2$  much further forward than usual. In contrast, the occipital cross-commissure in two other fishes from Achanarras (P. 17641, P. 17643, Text-figs. 23, 24), instead of its usual path  $Z-I_2-A-I_2-Z$ , misses  $I_2$  altogether, although these plates seem normally developed.

In P. 17641 (Text-fig. 23) K and X seem undoubtedly to have fused on the left side, but on the right K has been eliminated to the advantage of  $L_1$ , which is rather unusual (but see P. 6087, Text-fig. 15). Generally K is a better "stayer" than X, and it is worth noting that its division from J is often only superficial, the basal layers being completely fused (cf. Text-figs. 15, 22 etc.). On both sides the start of the infraorbital canal has been largely captured by  $Y_1$  and only a small subdivision of it is retained by X.

There is some doubt whether the missing plate on the right side is K or X, but the arrangement is partly paralleled in Text-fig. 15 where there was similar expansion of  $L_1$  into the K area and disarrangement of the canals.  $L_1$  and  $L_2$  in P. 17643 (Text-fig. 24) show a very obvious case of imperfect fusion.

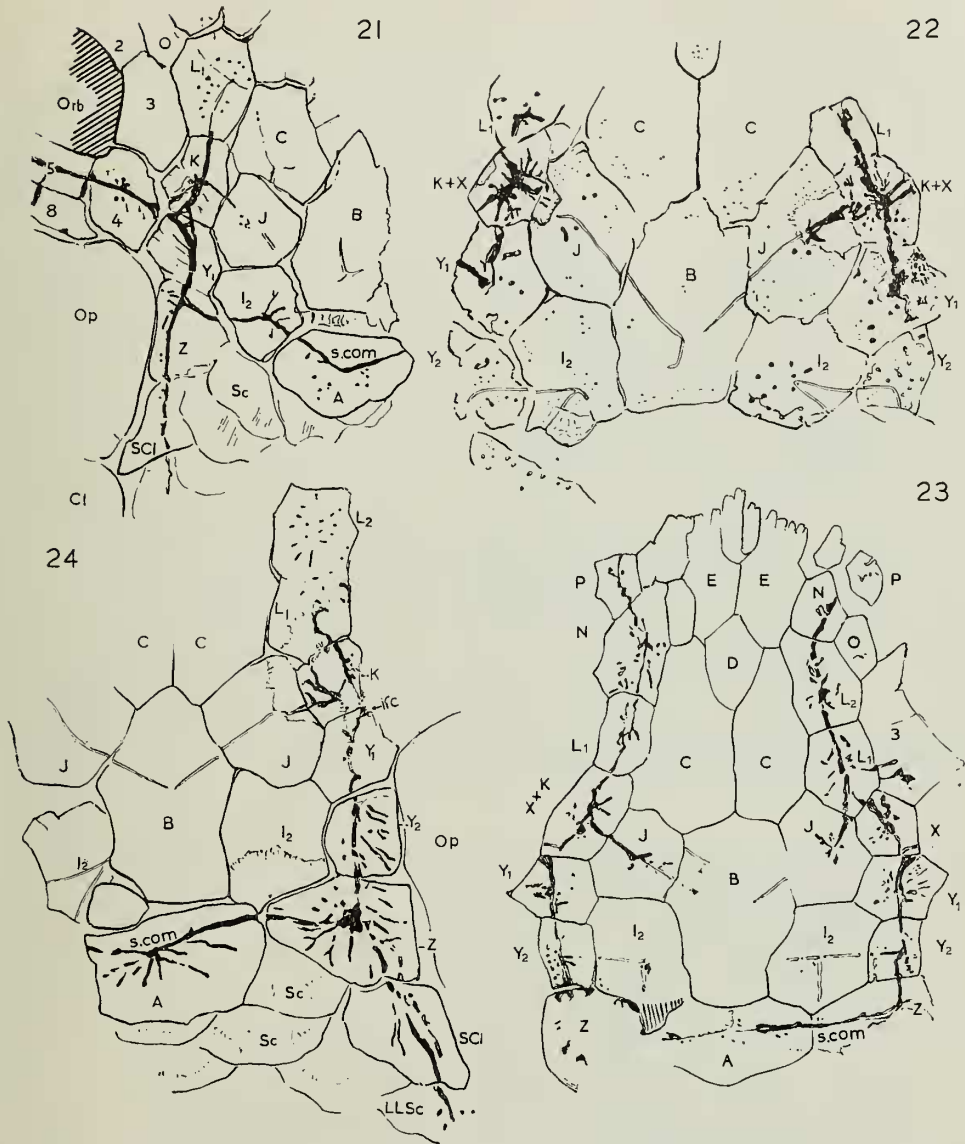
Of the two "brachypogopterus" types from Banniskirk illustrated (42480, R.S.M. 1859.33.624, Text-figs. 5, 6), the first shows a fairly obvious X and K fusion and the  $L_1-L_2$ , M and possibly N area is occupied by a single plate. The second shows a large N and on the left side only one small plate (labelled  $L_1$ ) between N and K, also a large  $Y_1$  and no  $Y_2$ . The naturally exposed sensory canals are standard as far as they may be traced.

#### *Attempts to Identify the Head-plates*

The difficulty of tracing the canals by the pores led Stensiö (*in* Holmgren & Stensiö 1936: 366, text-fig. 280A-C) to misplace the connection between the supraorbital canal and the main canal in the three rather difficult Edinburgh skulls on which he based his nomenclature (Text-figs. 25-27).

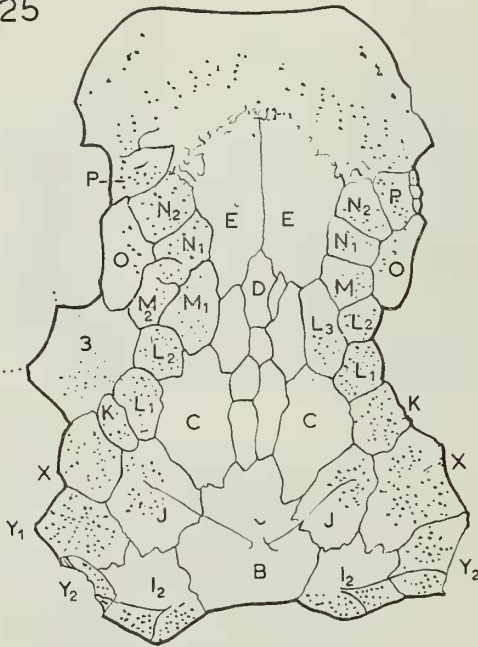
Stensiö's choice of a key-specimen (R.S.M. 1878.5.164) on which to base his identifications was not altogether fortunate, for it suffers very much from multiplication of plates in the central area and in the front lateral line series. His figure (Text-fig. 28), was formalized and partly restored, cf. Text-figs. 25, 29.

Neither of Stensiö's supraorbital bones ( $SO_1$ ,  $SO_2$ ) belongs to the circumorbital series, but his "dermosphenotic + postorbital" ( $Dsph + Po$ ) does, and the orbit is farther out and certainly smaller. This bone is not compound but is the circumorbital 3 of Forster-Cooper's notation. In the original specimen it is preserved only

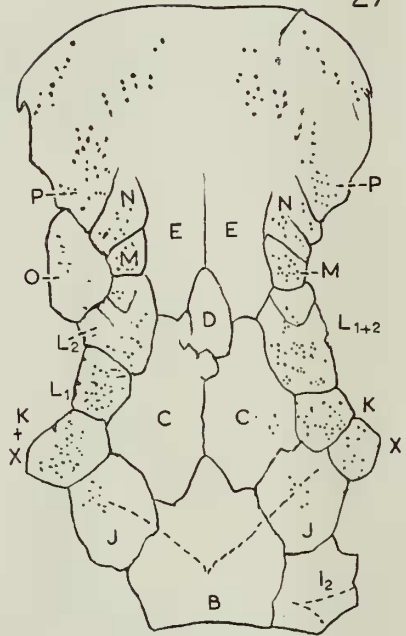


FIGS. 21-24. *Dipterus valenciennesi* S. & M. Fig. 21, Left posterior part of skull-roof and cheek with sensory canals dissected out (cf. Forster-Cooper 1937, pl. 5, fig. 9). Achanarras, Caithness. P.17642.  $\times 4$ . Cl, cleithrum. Op, operculum. Orb, orbit. Sc, scale (Forster-Cooper's "G"). SCI, supracleithrum. s.com, occipital cross-commissure. Fig. 22, Posterior half of much resorbed skull-roof with sensory canals partly dissected out to show probable fusion of plates K and X on each side. Killimster, near Wick, Caithness. 42403.  $\times 4$ . Fig. 23, Skull-roof with sensory canals dissected out (cf. Forster-Cooper 1937, pl. 6, fig. 11; Westoll 1949, text-fig. 2E). Achanarras, Caithness. P.17641.  $\times 2.5$ . s.com, occipital cross-commissure. Fig. 24, Right posterior part of skull-roof with sensory canals dissected out (cf. Forster-Cooper 1937, pl. 4, fig. 8). Achanarras, Caithness. P.17643.  $\times 2$ . ifc, infraorbital canal. LLSc, lateral line scale. Sc, body scale. SCI, supracleithrum. s.com, occipital cross-commissure.

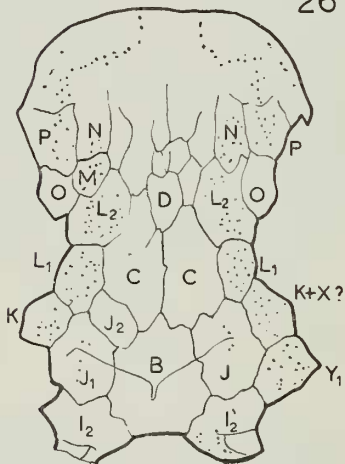
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FIGS. 25-27. *Dipterus valenciennesi* S. & M. Camera lucida drawings of originals of skull-roofs of "platycephalus" type, sketched by Stensiö (*in* Holmgren & Stensiö 1936: 366, text-figs. 280A-C). Fig. 25, Large head (6.1 cm. long) with median mosaic and unusually numerous plates (6) between K and P. Locality unknown. R.S.M. 1878.5.164.  $\times 1.3$ . Fig. 26, Medium sized head (4-6 cm. long) with anterior mosaic and only three plates between K and P on right side. Firth, Orkney. R.S.M. 1898.163.6.  $\times 1.3$ . Fig. 27, Large head (6.3 cm. long) showing tendency to subdivision of plates between K and P. Locality unknown. R.S.M. 1859.33.32.  $\times 1.3$ .

on the left side and carries an unusually large branch of the supraorbital canal, for as a rule the pores are few, often absent. This skull-roof, in spite of its oddities, is reasonably reduced to order under Parringtonian influence with Forster-Cooper's amended lettering (Text-fig. 25). The only point of real importance is that  $Y_1$ , normal on the left side, has most exceptionally not developed at all on the right side, where its place has been covered very largely by a much expanded X, and only to a small degree by the advance of  $Y_2$ .

Both of Stensiö's other two specimens show peculiar features. The small broad head (R.S.M. 1898.163.6, Text-fig. 26) shows division of J on the left, and no M and a possible fusion of K and X on the right; the larger head (R.S.M. 1859.33.32, Text-fig. 27) shows fusion of K and X on the left side, fusion of  $L_1$  and  $L_2$  and imperfect subdivision of N on the right.

Lehman (1959) in his work on the Upper Devonian Dipnoans from Greenland followed Stensiö in endeavouring to name the plates of the skull-roof, although by no means agreeing on the terms to be used, nor for that matter on the homologies when he did.

Comparison of Text-figs. 28–30 well illustrates the confusion that can be caused by efforts to identify these head-plates with the bones of other fishes.

Stensiö's supposedly compound "dermosphenotic and postorbital" (*Dsph* + *Po*, Text-fig. 28) is not the homologue even in part of Lehman's "Dermosphénotique" (*Dsph*, Text-fig. 30), as a glance at Text-fig. 29 will show, for Stensiö's plate is a simple circumorbital, no. 3 of Forster-Cooper. Lehman's "Dermosphénotique" is a single-centred plate (Lehman 1959, pls. 1–14, 16) and represents the survivor of K or X, probably K, which has taken over the other's territory and acquired all the canals (cf. Text-figs. 19, 20, 24). It is therefore strictly homologous with the most posterior member of Stensiö's "laterale Frontalserie" (*Fr. l*, Text-fig. 28) of which Lehman's "Nasaux" are the front members.

Again, Stensiö's supposedly compound "Supratemporo-Intertemporale" (*It* + *St*, Text-fig. 28) is also a simple bone, the X of Text-figs. 25, 29, which has invaded  $Y_1$ 's territory, and  $Y_1$ , the equivalent of Lehman's "Dermoptérotique antérieure" (*Dpt. 1*) has most exceptionally not developed at all. But Lehman's "Dermoptérotique postérieure" (*Dpt. 2*) is the  $Y_2$  of Text-fig. 29, and thus the homologue of Stensiö's "laterale freie Extraskapularplatte" (*Ext. l<sub>2</sub>*, Text-fig. 28). This last plate, which is laterally imperfect in the original (Text-fig. 25) does not show any part of the supratemporal cross-commissure as indicated by Stensiö (Text-fig. 28); it would have been present on the plate behind (*Z*), which is missing.

Stensiö's "hintere laterale Parietalplatte + einer lateralen Extraskapularplatte" (*Pa. l<sub>2</sub>* + *Ext. l<sub>1</sub>*, Text-fig. 28) which is identical with Lehman's "pariétolatero-extrascapulaire" (*PalExSc*, Text-fig. 30; Lehman, 1959: 18, pls. 1–21, text-figs. 2, 4, 5, 7–13, 21–23, 26), presents a very different problem, and indeed provides the key to the homologies of the plates of the earlier Dipnoi. These paired plates are the  $I_2$  of Text-fig. 29 and show in the available material of *Dipterus* and Lehman's illustrations a single growth centre; nevertheless the suggestion that there is an extrascapular element is supported by Westoll (1947: 134, text-fig. 31) who states that "it is likely that at least bone I also arose from more than one rudiment since a few specimens show ossicles enclosing the appropriate section of the canal". And



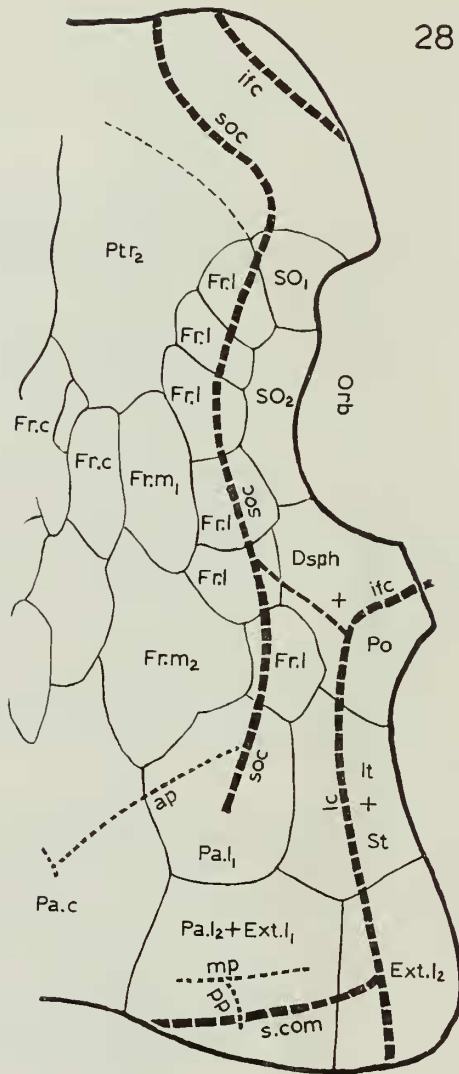


FIG. 28. *Dipterus valenciennesi* S. & M. Right side of Stensiö's diagram, text-fig. 280A (see Fig. 25), with original lettering.

*Dsph* + *Po*, Dermosphentiko-Postorbitale; *Ext. l2*, laterale freie Extraskapularplatte; *Fr.c*, zentrale Frontalserie; *Fr.l*, laterale Frontalserie; *Fr.m1*, *Fr.m2*, Platten der medialen Frontalserie; *It*, Intertemporale; *It* + *St*, Supratemporo-Intertemporale; *Pa.c*, zentrales Parietale; *Pa.l1*, vordere Platte der lateralen Parietalserie; *Pa.l2* + *Ext.l1*, laterale Parietalplatte + einer lateralen Extraskapularplatte; *Ptr2*, hintere Postrostralia; *SO1*, *SO2*, Platten der Supraorbitalserie (*S.O.* (=3) is omitted in Fig. 30); *ap*, vordere "Pitlinie"; *ifc*, Infraorbitalkanal; *mp*, mittlere "Pitlinie"; *pp*, hintere "Pitlinie"; *s.com*, Supratemporalokommissur; *soc*, Supraorbitalkanal.

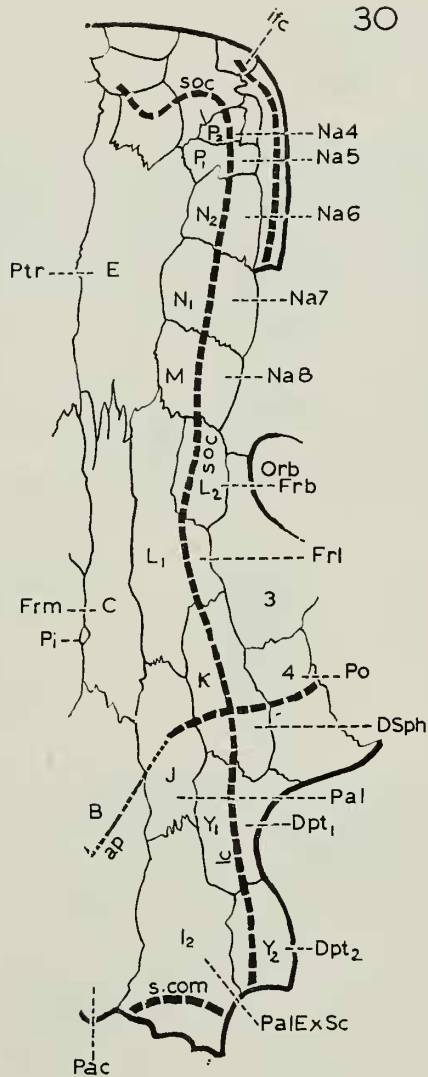
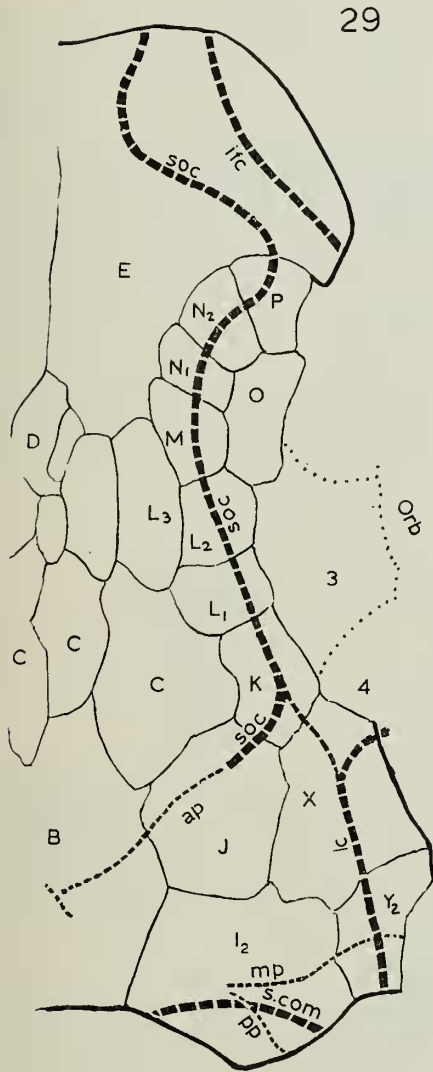


FIG. 29. *Dipterus valenciennesi* S. & M. Right side of same diagram (Fig. 28) partly redrawn from original specimen (cf. Fig. 25), with new interpretation of sensory canals and plates re-lettered according to modified FCAN. Other lettering as in Fig. 28.

FIG. 30. *Soederberghia groenlandica* Lehman. Right side of diagram of skull-roof by Lehman (1959, text-fig. 2) showing original lettering (with broken indication lines) and also modified FCAN.

*Dpt*<sub>1</sub>, dermoptérotique antérieure; *Dpt*<sub>2</sub>, dermoptérotique postérieure; *DSph*, dermosphénotique; *Frb*, composant antérieur distinct du frontal latéral; *Frl*, frontal latéral; *Frm*, frontal médian; *Na*<sub>1</sub>-*Na*<sub>8</sub>, nasaux; *Orb*, orbite; *Pac*, pariétal central; *Pal*, pariétal latéral; *PalExSc*, pariéto-latéroextrascapulaire; *Pi*, plaque pinéale; *Po*, postorbitaux; *Ptr*, postrostral; *So*, supraorbital. Sensory canals as in Fig. 28.



indeed the Belgian specimen of *Rhinodipterus secans* (White 1962 : 3, pl. 1, text-fig. 1) shows a similar "extra" plate enclosing the canal. Subdivision or proliferation of lateral line and general plates is not necessarily significant except that perhaps it points to the ancestral mosaic, and is of common occurrence in *Dipterus*, as the front of Stensiö's specimen shows. But in this instance it throws light on the presence of part of the commissure on  $I_2$  which is anomalous, for it is clearly out of line. This points to the former presence of a plate on each side between A and Z, now lost, and that the section of the cross-commissure belonging to it has been captured by  $I_2$ , that is, usually, for as noted above (p. 18, Text-figs. 23, 24) the commissure does sometimes go straight across through Z-A-Z, as it must have done when there were five plates in the "extrascapular" series, even as Säve-Söderbergh (1932 : 98, text-figs. 18, 20) postulated for his "common ancestor" of the ichthyostegids and crossopterygians; but it was not the bone  $I_2$  (Säve-Söderbergh's and Stensiö's  $Pa.l_2 + Ext.l_1$ ) that belonged to that row and originally bore the commissure, but a plate behind it, represented rarely by the little plate  $I_1$ , noted by Westoll, and seen also in *Rhinodipterus*.

The above correlations may be summarized as follows :

Stensiö 1936	Forster-Cooper 1937 emend.	Lehman 1959
(Text-fig. 28)	(Text-fig. 29)	(Text-fig. 30)
<i>Dsph + Po</i>	(CO) 3	SO (omitted)
(Posterior) <i>Fr. l</i>	K	<i>DSph</i>
<i>It + St</i>	X	absent
absent	absent ( $Y_1$ )	<i>Dpt_1</i>
<i>Ext. l_2</i>	$Y_2$	<i>Dpt_2</i>
<i>Pa.l_2 + Ext. l_1</i>	$I_2$	<i>PalExSc</i>

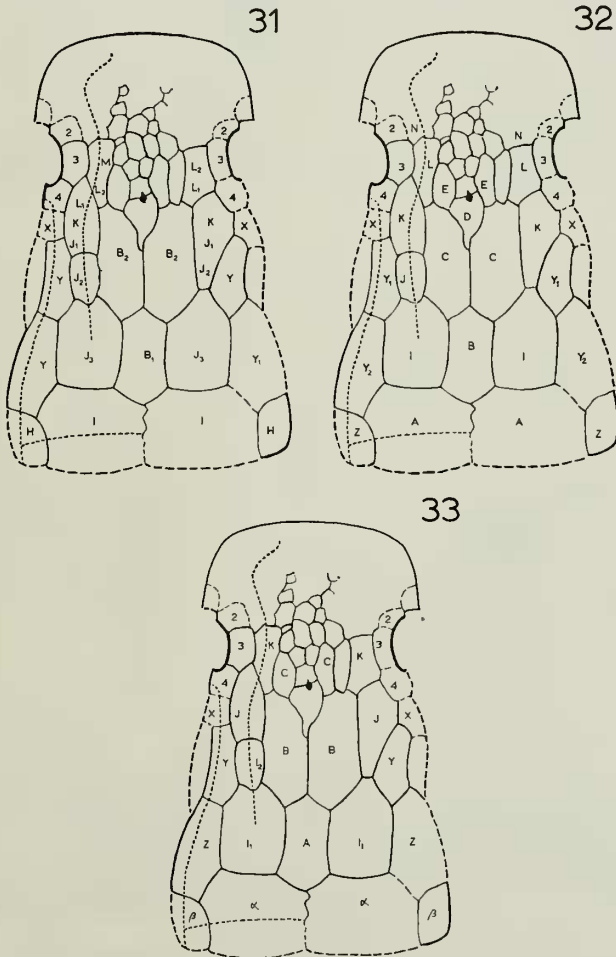
To trace back the homologues of the skull-plates of *Dipterus* in the earlier genera of dipnoans, the two species of *Dipnorhynchus* from the Lower Devonian (Siegenian)<sup>1</sup>, presents considerable difficulties. The roof-patterns of *D. süssmilchi* and *D. lehmanni* are reasonably well known, thanks to E. S. Hills (1941, pl. 9, text-fig. 5; 1943, text-fig. 1B), Westoll (1949 : 140-143, text-fig. 5) and Lehmann & Westoll (1952, pl. 24, fig. A, text-figs. 4A, 5A).

The most obvious points about the pattern of these skull-roofs (Text-figs. 31, 34) is the presence of a pineal foramen and the separateness of the supraorbital and infraorbital sensory canals. The back row of plates, presumably the extrascapulars, were finally shown in *D. lehmanni* (Text-fig. 31) to consist of two pairs of plates identified as H(Z), the smaller outside pair, and I, the large median pair, instead of the Z-A-Z arrangement of *Dipterus*. The occipital cross-commissure, apparently not seen in either specimen is assumed to run across H(Z)-I-I-(Z)H. There is no A plate but that immediately in front, a smallish median element, is considered to be B, and in front of that again a pair of larger plates completely separate in the German species, but partly attached to one another in the Australian. Westoll (1949 : 141) has resisted the temptation to label these as the "C" pair, as at first sight would seem obvious, on the grounds of their posterior relationship to the orbits and then to bones of the X-K area. This pair is labelled  $B_2$  and along side the B

<sup>1</sup> G. M. Philip & A. E. H. Pedder (1964 : 1323).

plates and bearing the supraorbital canal are L, K and three J plates on each side, separate in *D. süssmilchi*, or partly fused in *D. lehmanni*, the most posterior of the J plates being very large (Lehmann 1956, text-figs. 1, 2). It is unexpected that B should be in three parts, two paired, and at least two other arrangements seem possible.

Taking first the obvious one rejected by Westoll (Text-fig. 32) one might consider that in the later *Dipterus* the orbits had moved backwards from their position in *Dipnorhynchus*, bringing them opposite the anterior ends of the C plates (Text-fig. 35), and this would account for the difference in the relative position of K, X etc. in the two genera; and their movements outside of J might have been a factor



FIGS. 31-33. *Dipnorhynchus lehmanni* Westoll. Fig. 31, Reconstruction of skull-roof after Lehmann & Westoll (1952 : 411, text-fig. 5A) with the original lettering (anterior Y-plates should be  $Y_2$ , posterior,  $Y_1$ ). Fig. 32, The same, but re-lettered according to first alternative. Fig. 33, the same, but re-lettered according to second alternative.

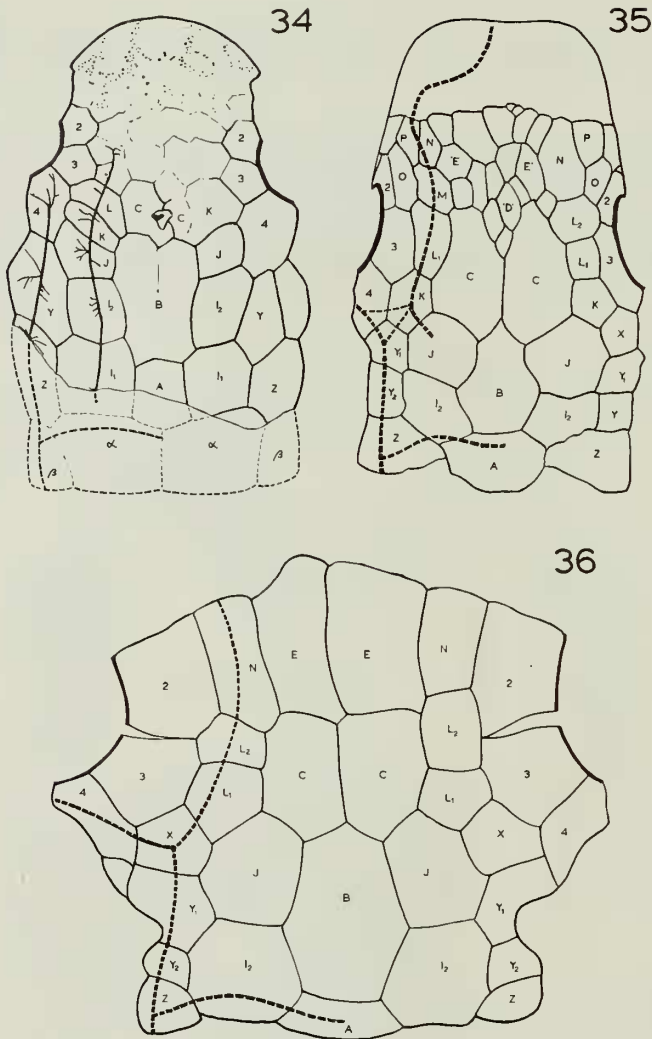


FIG. 34. *Dipnorhynchus süssmilchi* (Etheridge). Outline reconstruction of skull-roof, after Hills (1933 : 637, text-fig. 2) with addition of the sensory canals from Hills (1941 : 646, text-fig. 1) and the back of the skull-roof restored in outline, after Westoll (1949 : 142). The lettering according to second alternative (cf. Fig. 33).

FIG. 35. *Dipterus valenciennesi* S. & M. Reconstruction of skull-roof, after Graham-Smith & Westoll (1937, text-fig. 2a) and Westoll (1949, text-fig. 1A), the lettering modified after Fig. 18.

FIG. 36. *Scaumenacia curta* (Whiteaves). Reconstruction of skull-roof, after Westoll (1949, text-fig. 6D) with the lettering modified.

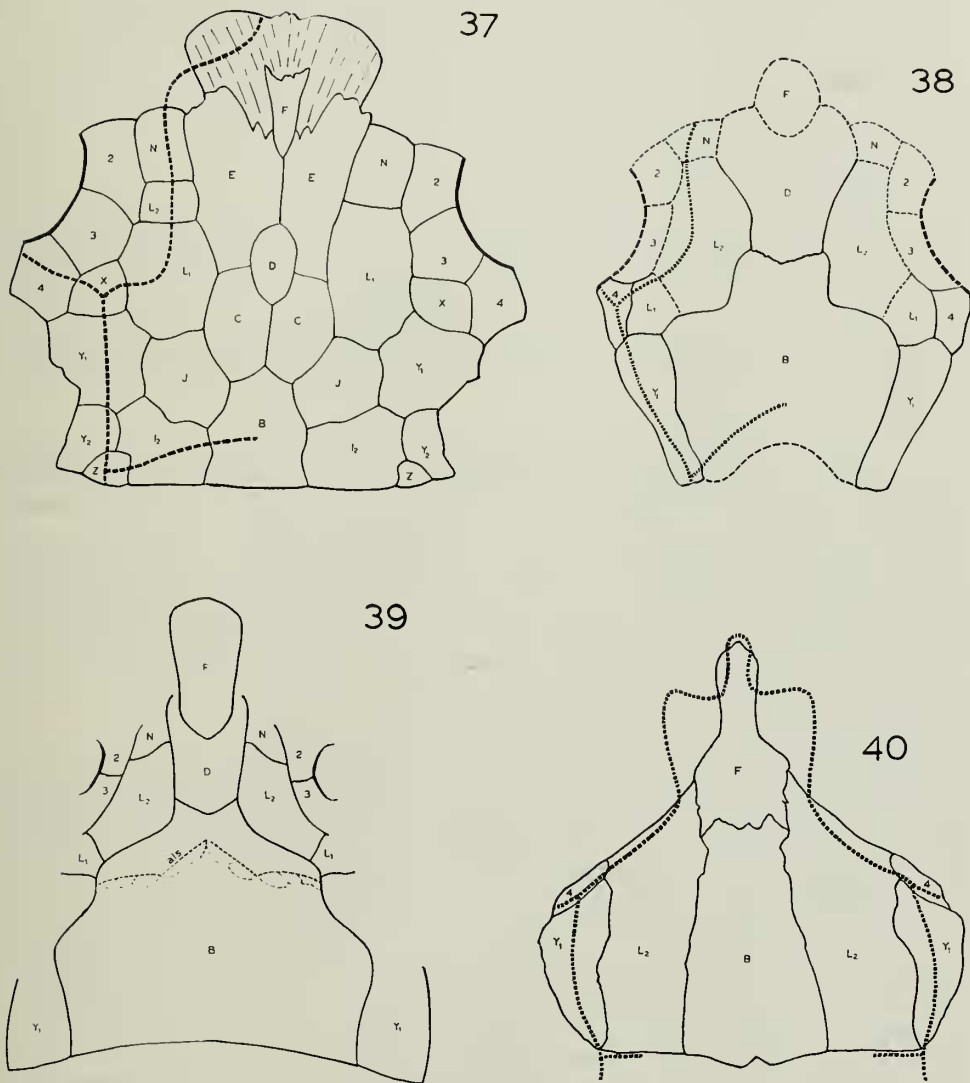


FIG. 37. *Ctenodus cristatus* Agassiz. Reconstruction of skull-roof, after Westoll (1949, text-fig. B) with the lettering modified, and Watson & Gill (1923, text-fig. 21).

FIG. 38. *Ceratodus sturi* Teller. Reconstruction of skull-roof, after Westoll (1949, text-fig. 9A), with lettering modified.

FIG. 39. *Ceratodus formosus* Wade. Reconstruction of skull-roof. *als*, approximate anterior limit of scale covering.

FIG. 40. *Neoceratodus forsteri* (Kreffft). Skull-roof, after Holmgren & Stensiö (1936, text-fig. 288B), re-lettered.

contributory to the anastomosing of the infraorbital and supraorbital canals. The paired "B<sub>2</sub>" plates would then be C plates and instead of a proliferation of J plates we would have a more normal series of K, J and I. B would be small and A unaccounted for, unless it was the result of fusion of the very large paired plates labelled I by Westoll, for it seems unlikely in any event that the supposed I plates would later move forwards from the "extrascapular" row to embed themselves in the skull-roof between B and Y as in *Dipterus*.

On the other hand, if we accept the possibility that the two anterior B<sub>2</sub> plates of Westoll's interpretation did fuse to form the B of *Dipterus*, as seems indicated in *Dipnorhynchus süssmilchi* (Text-fig. 34), then an even more interesting situation could have held (Text-fig. 33). B, of Westoll, would be A and J<sub>2</sub> would be I<sub>2</sub> (missing on the right side) with J<sub>3</sub> as I<sub>1</sub>, the plate that is still occasionally preserved as a small entity carrying part of the occipital cross-commissure in *Rhinodipterus* (White 1962, pl. 1, text-figs. 1, 2) and *Dipterus* (Westoll 1949, text-fig. 3I). On the outside of it is Z(H).

At this level of development, which Westoll (1942 : 142) claims is a fair approximation to the hypothetical ancestral condition, this row did not carry the cross-commissure, which was supposedly borne by the row behind, H-I-I-H of Westoll (Text-fig. 3I), but here supposed to be a row of plates ( $\beta$ - $\alpha$ - $\alpha$ - $\beta$ , Text-figs. 33, 34) that has now disappeared in other known fishes. This is in keeping with the important point shown by Westoll (1938, text-fig. 2) in his brief paper on the ancestry of the Tetrapods, that in vertebrates there is a movement backwards of the bones of the skull roof with additions at the anterior end by orderly development from the variables, and a loss of those behind with a shortening of the occipital region, features shown in some degree by *Dipterus* relatively to *Dipnorhynchus*.

Between *Dipnorhynchus* and *Dipterus* there must have been a stage when the hindmost row  $\beta$ - $\alpha$ - $\alpha$ - $\beta$  was lost and the cross-commissure had been taken over by the full "extrascapular" row Z-I<sub>1</sub>-A-I<sub>1</sub>-Z, before the two I<sub>1</sub> plates lost their territory to their neighbours and their remnants fused with I<sub>2</sub> in front taking with them a segment of the commissure—as noted above, only rarely does this remnant of I<sub>1</sub> ever show itself as a minute independent plate.

From *Dipterus* one can move forward in time through a perfect morphological series based on Westoll's (1949, text-figs. 6D, 8B, 9A) outline restorations of the later dipnoans *Scaumenacia*, *Ctenodus* and *Ceratodus*, which show progressive diminution and final loss of the "extrascapular" Z-A-Z row, with the cross-commissure being finally captured by Y<sub>1</sub>-B-Y<sub>1</sub> (Text-figs. 35-39). At the same time the series shows one other powerful trend coupled with the relative movement back of the head plates, and that is on simplification of the pattern, by invasion and loss rather than by fusion as Westoll indicates by his lettering. This trend is after all a continuation of the process seen in passing from *Dipnorhynchus* to *Dipterus*. The apparently unstable many plated mosaic inherited from the ancestral form persists in the CDE area in *Dipnorhynchus*; in *Dipterus* the C area generally, and that of D and E quite often, has settled down in a more constant pattern of a few large plates, which is characteristic of the later terms in the series. It is interesting to note that in *C. formosus* Wade (1935 : 1, pl. 1; see also Text-fig. 39) the dermal skull pattern can be reasonably interpreted in a form comparable with that of *C. sturi* Teller from



slightly earlier beds in the Austrian Alps (Text-fig. 38), the most striking difference being that F has increased in size at the expense of D, which in the living *Neoceratodus* has disappeared altogether (Text-fig. 40).

The various trends in this morphological series may be summarized as follows :

	Age	Posterior row of plates	Centre plates front to rear	Lateral line plates, $\beta$ -X, $\alpha$ -P
<i>Dipnorhynchus lehmanni</i>	late Lower Devonian	$\alpha\beta\beta\alpha$	Ant. mosaic BA $\alpha$	4, 4
<i>D. süssmilchi</i> . . .	do.	$\alpha\beta\beta\alpha$	Ant. mosaic BA $\alpha$	3, 7 +
<i>Dipterus</i> . . .	Upper M.O.R.S.	ZAZ	Ant. mosaic CBA or FEDCBA	4, 7
<i>Scaumenacia</i> . . .	Early U.O.R.S.	ZI <sub>2</sub> AI <sub>2</sub> Z	ECBA	4, 3
<i>Clenodus</i> . . .	U. Carboniferous	Y <sub>2</sub> ZI <sub>2</sub> BI <sub>2</sub> ZY <sub>2</sub>	FEDCB	4, 3
<i>Ceratodus sturi</i> . . .	M. Trias	Y <sub>1</sub> BY <sub>1</sub>	FDB	1, 3
<i>C. formosus</i> . . .	M. Trias	Y <sub>1</sub> BY <sub>1</sub>	FDB	1, 3
<i>Neoceratodus</i> . . .	Living		FB	1, 1

### *The Endocranium*

The undersurface of the skull of *Dipterus* has been tolerably well known since the days of Hugh Miller (1849 : 62, text-fig. 20). Pander (1858 : 10, pl. 3, figs. 11, 13, 14) was the first to deal seriously with this part ; Traquair (1878 : 5, pl. 3, fig. 1) established that the suspension was autostylic ; then Woodward (1891 : 234, text-fig. 36(i)) gave a restoration of the upper and lower jaws, and Goodrich (1909 : 242, text-fig. 210A) one of the whole palate. Finally Watson & Day (1916 : 29, text-fig. 6) published a general description of the palatal aspect of the head with an unlettered restoration which has been freely copied by later authors, either as originally published (Holmgren & Stensiö 1936 : 365, text-fig. 279) or somewhat modified (Graham-Smith & Westoll 1937 : 251, text-fig. 8D). Säve-Söderbergh (1952 : 22) noted further details “. . . similar canals [to those of *Chirodipterus*] for the efferent pseudobranchial arteries, grooves for the lateral dorsal aortae and orbital arteries, canals for occipital arteries, and grooves for the internal jugular veins”, but he gave no figures. Two years later Jarvik (1954 : 69, text-fig. 36B) figured a fine specimen in which he labelled the foramen for the occipital artery, a large paired fossa on the lower side of the otic region, and the groove for the lateral dorsal aorta.

Kesteven (1951 : 108) has given a clear warning against the too positive identification of foramina and other features in fossil skulls. The force of this warning is proportional to the distance in the relationship between the fossil and a living species. In the case of the Dipnoi, it can be shown that the endocranium of *Dipterus* is sufficiently close to the only other described fossil Dipnoan skull, that of the Upper

Devonian *Chirodipterus* (Säve-Söderbergh 1952)<sup>1</sup> and to that of the living *Neoceratodus* (Günther 1871; Huxley 1876; Kesteven 1931; Holmgren & Stensiö 1936: 372) that comparisons may be reasonably made.

The most important specimen of *Dipterus* is an incomplete but uncrushed skull from "Caithness", P. 17410, with a curiously asymmetrical pattern to its roof-plates (Text-figs. 42-47). This has lost the snout and most of the right side of the skull roof and endocranium, but the left side is reasonably well preserved, although the perichondral bone has flaked off in places and intractable matrix obscured others. The articular head of the left palatoquadrate is displaced upwards. This

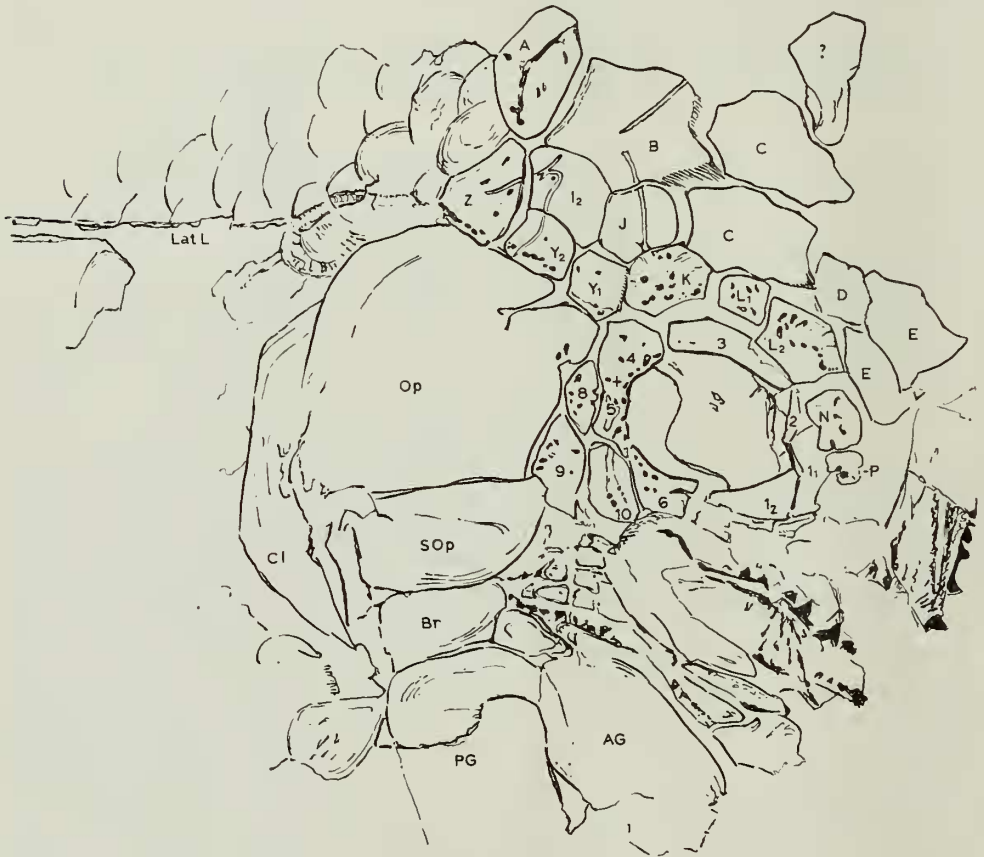


FIG. 41. *Dipterus valenciennesi* S. & M. Head of small specimen showing part of lower dentition of each side. Achanarras, Caithness. P. 22194.  $\times 5$ . AG, anterior gular; Br, branchiostegal ray; Cl, cleithrum; LatL, lateral line; Op, operculum; PG, posterior gular; SOp, suboperculum.

<sup>1</sup> Säve-Söderbergh pointed out (p. 8) that the snout of *Chirodipterus* if broken off would be identical with the fossils described as *Ganorhynchus*. The locality and formation of the unique holotype (44627) of the type-species, *G. woodwardi* Traquair (1873: 555, pl. 14) are unrecorded, but Mr. H. A. Toombs has established that the matrix is so similar to that of Middle Devonian (Couvinian) fossils from the neighbourhood of Gerolstein in the Eifel as to leave little doubt as to its source.



skull was most probably developed by Säve-Söderbergh and formed the basis of his brief remarks on the endocranium of *Dipterus* (1952 : 22) in his classical description of the skull of *Chirodipterus*.

The bony structure of the endocranium is exactly as that described in *Chirodipterus* (Säve-Söderbergh 1952 : 6) consisting of inner and outer shells of thin laminar perichondral bone which also lined the vascular and nerve canals connecting the two capsules. The space between is largely filled by cancellar bone. The latter is frequently exposed in this specimen owing to the loss of the perichondral layer, and it is not always a simple matter to determine whether the supposed foramina are genuine or not. As often observed in this genus and noted in *Chirodipterus* the neurocranium is undivided and forms a single unit with the palatoquadrates which

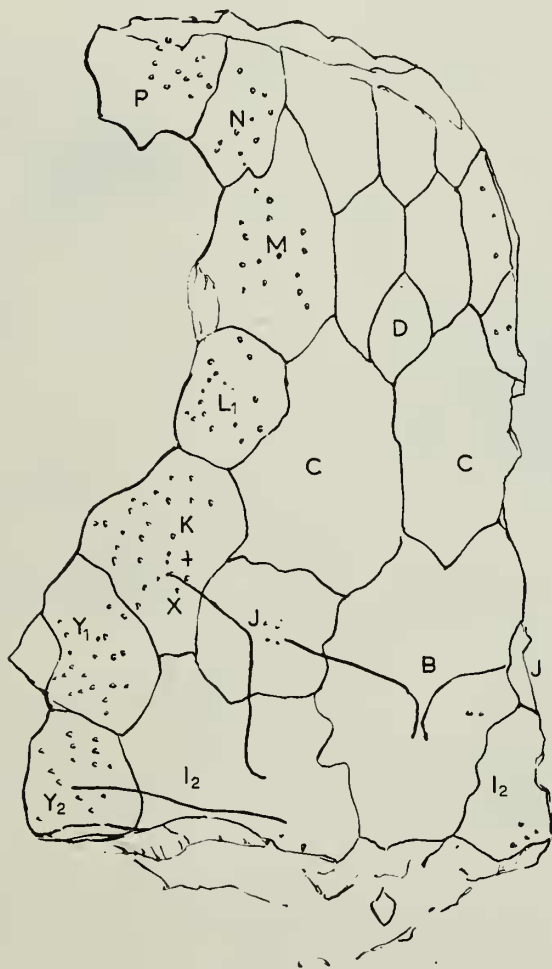
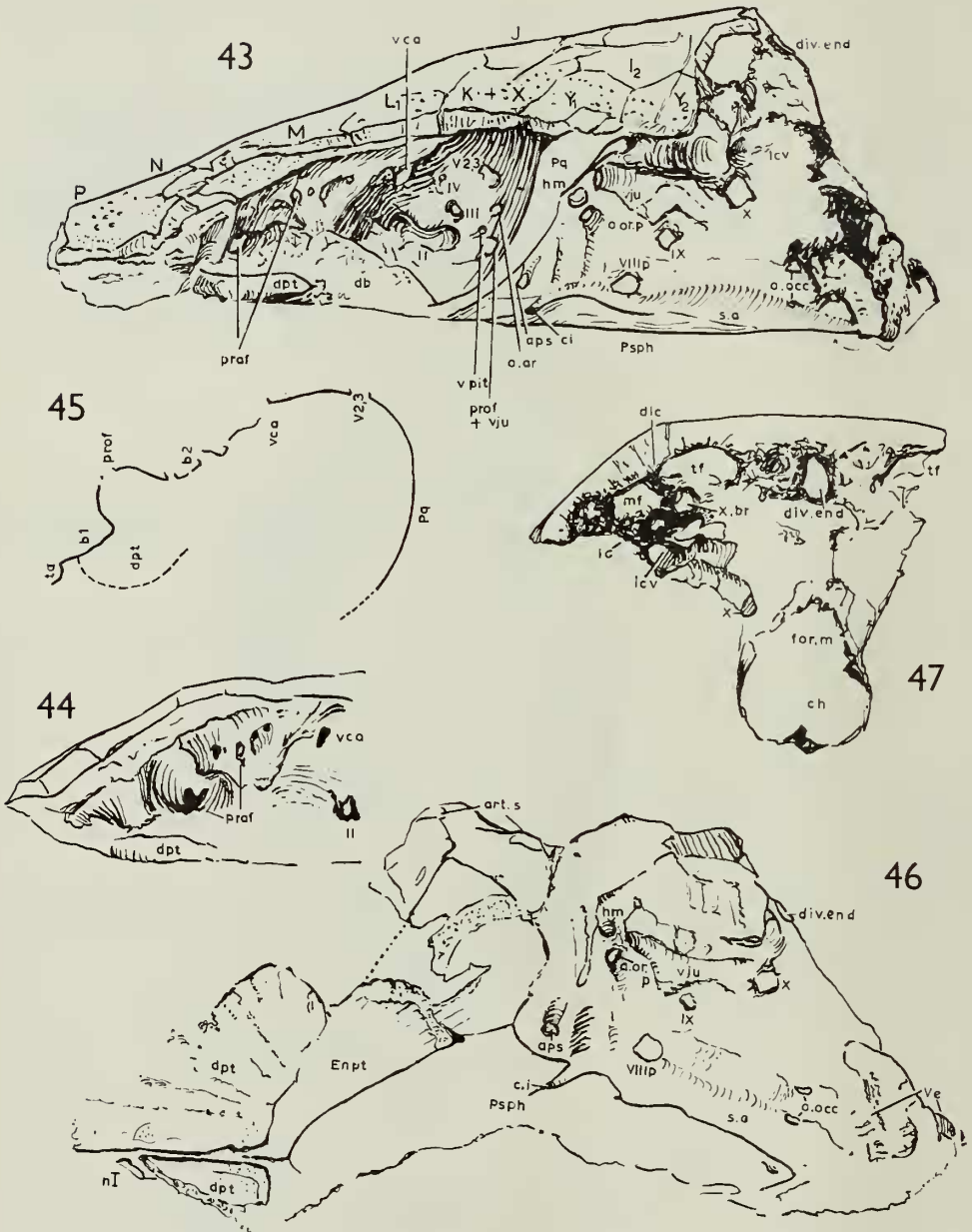


FIG. 42. *Dipterus valenciennesi* S. & M. Imperfect and irregular skull-roof. Same specimen (P.17410) as in Figs. 43-47.  $\times 2.5$ .



FIGS. 43-47. *Dipterus valenciennesi* S. & M. Imperfect skull. Locality in Caithness unknown. P.17410. Fig. 43, Left side view. Palatoquadrate removed.  $\times 2.5$ . Fig. 44, Planum antorbitale.  $\times < 4$ . Fig. 45, Outline of left orbitotemporal space.  $\times 2.5$ . Fig. 46, Three-quarters ventral view.  $\times 2.5$ . Fig. 47, Back of skull.  $\times 2.5$ . *a.occ*, foramen for occipital artery; *a.or*, foramen for orbital artery; *a.or.p*, posterior opening for orbital artery; *aps*, posterior opening of efferent pseudobranchial artery;

form on each side a high transverse lamina, in this specimen with a forward slope of about  $45^\circ$ . A major difference between the skulls of *Dipterus* and *Chirodipterus* is that in the former the neurocranium is in contact with the cranial roof throughout its length, so there is no median fossa or crest over the otic and occipital regions, the fossa for the temporal muscle (*tf*) on each side being bounded by the neurocranial wall medially and by the thin dorso-lateral crest (*dlc*) on the outer side (P. 17410, Text-fig. 47). This crest is probably continued backwards under the "tabular horn" which is a projection of plate  $I_2$  itself and seems to comprise all three layers (P. 46761, Pl. 3, figs. 1, 2).

The lateral crest (*lc*), in continuation of the palatoquadrate, forms the outer wall of the masseter fossa (*mf*) on the inside and the roof of the branchial cavity on the outer.

Of the ethmoid region in front of the planum antorbitale there remains only a short length and cross-section of the perichondral lining of the right olfactory canal (*nI*, Text-fig. 46), through the post-nasal wall, and it is clear that, as in *Chirodipterus*, ossification was in this part only perichondral. The anterior ramifications of the profundus in the roof of the nasal capsules along with other canals and vessels, are well displayed in R.S.M. 1859.33.612, and to a lesser extent in P. 46693.

The ethmoidal part of the orbital space, preserved only on the left side, is very different from that of *Chirodipterus* or *Neoceratodus* (Text-figs. 43-45), for it is much longer, occupying as much of the space as the orbito-temporal region. The posterior face of the planum antorbitale is completely ossified and runs diagonally from the outer margin backwards and inwards to the neurocranial wall. The outermost part is formed by a very large buttress ( $b_1$ ) which joined the entopterygoid to support the dental plate. Narrow at the base it had a wide triangular section dorsally and a small space-filling talon (*ta*) outside it. Separated from it by a deep cavity containing the main profundus foramen (*prof*) was an even larger multiple buttress ( $b_2$ ) forming the neurocranial wall and pierced by two or three small foramina for branches of the profundus. The lower half of this region, which is probably a little crushed downwards, is obscured by débris (*de*), but a diagonal fracture in P. 755, apparently through the second buttress immediately above the inner posterior angle of the left tooth-plate shows the buttress passing below into a horizontal lateral shelf above the entopterygoid.

These buttresses provide a necessary support, from the skull-roof, to massive

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*art.s.*, articular surface of palatoquadrate;  $b_1, b_2$ , buttresses; *ch*, notochord; *c.i.*, groove for internal carotid; *db*, débris; *div.end.*, diverticulum of endolymphatic duct; *dlc*, dorso-lateral crest; *dpt*, tooth-plate; *Enpt*, entopterygoid; *for.m.*, foramen magnum; *hm*, exit of truncus hyomandibularis VII; *lc*, lateral crest; *lcv*, foramen for lateral cerebral vein; *mf*, masseter fossa; *Pq*, palatoquadrate (cut away in Fig. 43); *prof*, main profundus foramen; *prof + vju*, foramen for profundus nerve and jugular vein; *Psph*, parasphenoid; *s.a.*, groove for lateral dorsal aorta; *ta*, talon of buttress; *tf*, temporal fossa; *vca*, foramen for anterior cerebral vein; *Ve*, fused vertebra; *vju*, groove for internal jugular vein; *v.pit.*, groove and foramen for pituitary vein.

*nI*, olfactory nerve; *II*; *III*; *IV*;  $V_2, 3$ , opening for mandibular and maxillary branches of trigeminal nerve; *VIIIp*, posterior branch of acoustic nerve; *IX*; *X*; *Xbr*, branches of vagus.

dental plates, which with their strongly denticulated surfaces, were clearly capable of dealing with very rough food. Mollusca are not very evident in these beds, and such denticulated plates usually with no obvious facets of wear, speak rather for gripping and crushing struggling animal prey than for cutting inert vegetable matter, so arthropods, worms and perhaps other fishes suggest themselves. That *Chirodipterus* had feebly sculptured plates and rudimentary buttresses—Säve-Söderbergh (1952: II, pl. 3, fig. 2) speaks only of "a vertically elongated prominent area"—suggests that it fed on softer unresisting matter such as carrion. On the other hand the earlier Australian marine *Dipnorhynchus* had a large free buttress at the outer margin of the entopterygoid in the middle of the orbito-temporal space (P. 33699) to support its large massive dental plates for holding and crushing shelly prey, such as the numerous brachiopods with which its remains are associated.

Only the outer face of the left wall of the orbito-temporal region of the neurocranium of *Dipterus* is reasonably preserved (P. 17410, Text-fig. 43). The brain-case is short and narrow, and the wall, as preserved, curves gently inwards towards the skull roof. There is a wide subocular shelf, a continuation of that already noted, and this passes imperceptibly into the processes of the palatoquadrate. In front high up and just behind the second buttress is a large foramen for the anterior cerebral vein (*v.ca*). Below and behind this is a very large dumb-bell shaped aperture for the optic nerve (*II*). Whether this is its true shape is not quite certain, but if so, it is unlike what is found in either *Chirodipterus* or *Neoceratodus*. As in *Chirodipterus*, above and behind in a slanting line are three foramina, the topmost for the fourth nerve (*IV*), the middle and largest for the oculomotor (*III*); and on a level with the foramen for the optic nerve, a groove and foramen for the pituitary vein (*v.pit*). Immediately behind and below this vein is the large foramen for the profundus nerve and the internal jugular vein (*prof+v.ju*). This foramen lies at the junction of the endocranium and the fused processes of the palatoquadrate and faces forwards. High above this foramen is a large opening corresponding to that identified in *Chirodipterus* for the mandibular and maxillary branches of the trigeminal nerve (*V<sub>2,3</sub>*), but it is relatively farther back, and below it, instead of at the side, is the smaller foramen for the orbital artery (*a.or*).

Behind the palatoquadrate on the left side the ventro-lateral surface of the otic and occipital regions is reasonably well preserved (Text-figs. 43, 46, 47), although the upper part formed by the lateral crest (*lc*) is possibly a little distorted by crushing. Below it the wall of the endocranium is almost straight and vertical except for the slight swelling over the saccular division of the labyrinth cavity.

The back of the skull slopes somewhat irregularly at an average angle of 60° to the base of the occipital region as preserved, but although two vertebral elements (*Ve*) are seen to be incorporated in this part it is clearly imperfect.

A number of features are readily identifiable with those recognised in *Chirodipterus*.

Immediately above the labyrinth swelling lies the groove for the internal jugular vein (*v.ju*) which leads to the foramen piercing the palatoquadrate, and just in front of this foramen is another, almost as large, probably for the exit of the truncus hyomandibularis *VII(hm)*, and below it the posterior opening of the canal for the orbital artery (*a.or.p*) to which a groove leads from that of the dorsal aorta (*s.a*).



Where these two grooves meet a third groove, for the internal carotid artery, passes slightly medially into a notch (*ci*) and then under the parasphenoid. Above it is the posterior opening of the efferent pseudobranchial artery (*aps*). All these features are little more than a paraphrase of what has been found in *Chirodipterus*, but not seen in that genus is a very large opening, possibly enlarged by fracture, just behind the junction of these same three grooves, probably for a posterior branch of the acoustic nerve (*VIII $\beta$* ). Above and behind this is the foramen for the glosso-pharyngeal nerve (*IX*).

The short occipital region is continuous with the otic but the sides are flatter and more nearly vertical. Owing to the slope of the back of the head, about 60° but exaggerated by breakage, the dorsal flange formed by the lateral crest is present only in the anterior part.

At least two vertebrae are fused on to the basioccipital region, and in other specimens (DMSW.P. 149, Pl. 1, fig. 2; also P. 755 and R.S.M. 1859.33.617) it seems evident there are three.

The main features of the otic region, the internal jugular groove (*vju*) above and that of the lateral dorsal aorta (*s.a*) below, are continued on to the occipital region. The vagus foramen (*X*) is in the jugular groove in much the same position as in *Chirodipterus* (Säve-Söderbergh 1952 : 19, text-fig. 8). Immediately above and at right angles to it is a large foramen running into the back of the skull, presumably for the lateral cerebral vein (*lc $v$* , Text-figs. 43, 47), and above this are two smaller openings for branches of the vagus (*Xbr*). However, the most conspicuous feature in the back of the skull is a pear-shaped opening in the centre near the skull-roof, presumably a cross-section of a median diverticulum of the endolymphatic duct, (*div. end*) as in *Eusthenopteron* (Stensiö 1963 : 97, 100, text-figs. 50A, 51A).

The groove of the lateral dorsal aorta (*s.a*) widens to the rear and joins that of the right side behind the parasphenoid (P. 34549, Text-fig. 49; *cf.* Jarvik 1954, text-fig. 36B). Just before it does so, it is pierced at its upper margin by a foramen for the occipital artery (*a.occ*), which is nearly horizontal owing to the swelling out of the bone. It penetrates the bone for almost 3 mm. by a somewhat sinuous course, and re-emerges above and slightly behind by a similar foramen above, then continues upwards by a well-marked groove (P. 34544; also DMSW.P. 149) which apparently bifurcates before the vessel re-enters the skull through two distinct foramina (Text-fig. 48).

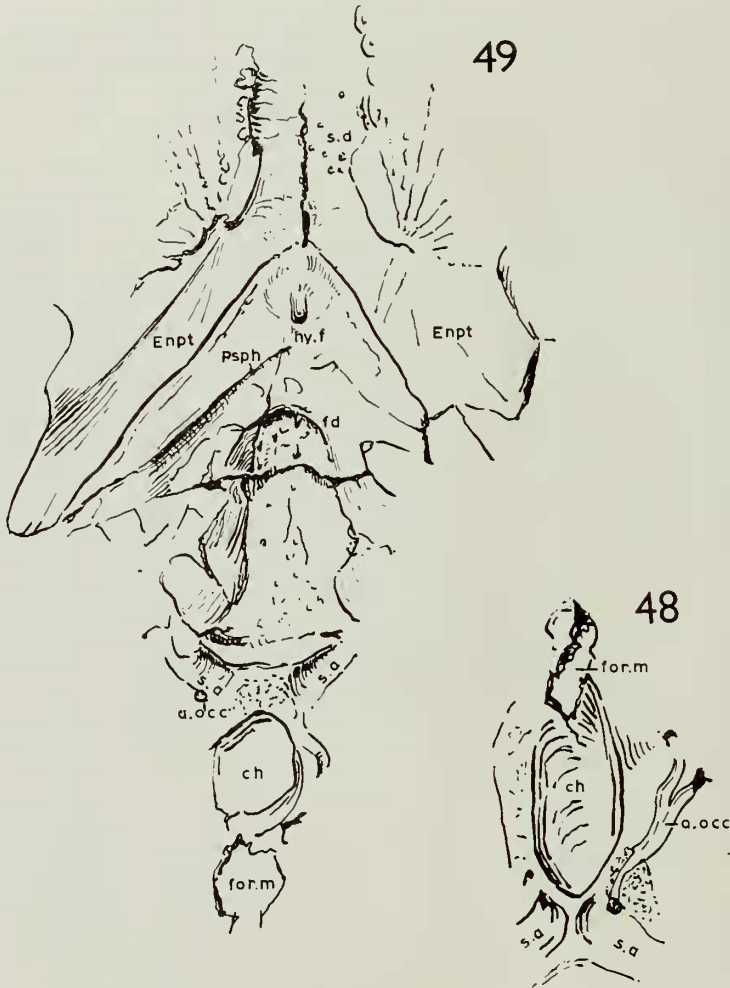
The right side of the occipital region of P. 17410 is too imperfect to show these features, but the vagus foramen, much enlarged, is present and a little below and behind it, as in *Chirodipterus*, two or three foramina for spino-occipital nerves.

Of the dermal bones of the palate in this specimen, only the right half of the parasphenoid and part of the right entopterygoid is preserved. The former is sunk into the endocranium so that the surfaces are level, and they give the impression of being joined by a suture; and the entopterygoid, to which the parasphenoid is truly sutured, has the same appearance in regard to the palatoquadrate.

The features of the palate are better seen in other specimens, in particular P. 34549, a specimen collected by Dr. D. L. Dineley in Clardon Haven, near Thurso (Text-fig. 49, Pl. 1, fig. 1). It is a crushed head with very well preserved, but flattened palate.



The anterior angle of the parasphenoid in this specimen shows a very well marked hypophysial foramen (*hy. f*) which runs inwards (upwards) and somewhat backwards. There is a broad, flat or slightly concave selvage along the antero-lateral sides which is widest in front medially and decreases laterally to vanish at the greatest breadth. On the medial side of this selvage the parasphenoid shows a complementary depression or groove, narrowest medially in front and widest behind at the lateral angle. Between these grooves the parasphenoid is gently convex. Near the front of this



Figs. 48, 49. *Dipterus valenciennesi* S. & M. Fig. 48, Basioccipital region to show course, partly excavated, of occipital artery (*a.occ*). Clardon Haven, near Thurso, Caithness. P.34544.  $\times 2.25$ . Fig. 49, Palatal view. See also Pl. I, fig. 1. Clardon Haven, near Thurso, Caithness. P.34549.  $\times 2.25$ . Both specimens cold. D. L. Dineley, 1957. *fd*, fold; *hy.f*, hypophysial foramen; *s.d*, secondary denticles. Other lettering as in Figs. 43-47.

median area and some distance behind the hypophysial foramen there is a very conspicuous crescentic, transverse slit or infolding of the surface of the parasphenoid directed forwards (*fd*) with a corresponding broad and shallow depression behind it in which are four or five well marked denticles on low ridges. The depth of the pocket cannot be seen, but probably it does not extend far in. It is seen in a few other specimens, in varying degrees of development; well developed although partly masked by transverse cracks in P.755, P.34556 and M.M. no. L.11577; irregular in R.S.M. 1859.33.614; replaced by a number of smaller shallow tucks in M.M. no. L.10861, and absent in R.S.M. 1859.33.33 (Traquair 1878, pl. 3, fig. 1) and other specimens. This feature is therefore no more than an individual defect, possibly based on an atrophied organ, in the laminar surface layer of the parasphenoid, which is frequently wrinkled or irregular when worn (P.34549 and DMSW.P.149, Pl. 1, figs. 1, 2) and possibly was denticulated over much of the palatal surface (M.M. no. L.11577).

The hypophysial foramen varies quite obviously in its development, being conspicuous in some specimens (Pl. 1, fig. 1) but in others reduced to a very small size and accompanied by other diminutive foramina (P.34556). It was figured without comment by both Pander (1858, pl. 3, figs. 11, 13) and Günther (1871, pl. 34, fig. 4) and has been noted by Westoll (1949, text-fig. 1D). It is also present in one of the specimens of *Rhinodipterus secans*, but Gross (1956 : 28, text-fig. 21c) dismissed it as "vielleicht sekundär entstanden". No such foramen has been recorded from Upper Devonian dipnoans.

The dental plates are continuous with the entopterygoids and appear as mere outgrowths of the supporting bones. Fine new specimens of the mandible of the earlier *Dipnorhynchus* from New South Wales (P.33714, P.46773) clearly show that the rather formless swellings that do duty as dental plates are in fact just thickenings of the vascular and cosmine layers of the bone of the jaw, and it is evident the more definitely patterned "plates" of *Dipterus* and later dipnoans are of like origin. In well preserved specimens they are clearly differentiated by their thick surface layer, which has much the same appearance as the cosmine of the external head-bones but with rather fewer openings of the fine tubuli, well marked in the low flat longitudinal medial areas along which the two plates meet (P.34543, Pl. 2, figs. 1, 2; R.S.M. 1859.33.33, Traquair 1878, pl. 3, fig. 1). In P.755 and 33166 (Pl. 2, figs. 3, 4) there is irregularity along the symphyseal margin due to resorption and in P.34556 (Pl. 2, fig. 5) as in P.46691 and R.S.M. 1859.33.612, much of the thick cosmine layer has disappeared showing underlying trabecular layer. In extreme cases not only has the whole of the surface between the dental plates gone, as in the relatively small original of Pl. 1, fig. 2 (DMSW, P.149), but secondary tubercles (*s.d.*) may be developed on the rough trabecular bone, and an unusual number of denticles appear between the regular rows on the biting surfaces (P.34549, Pl. 1, fig. 1, Text-fig. 49). In this specimen small irregular areas of the right dental plate (left of figure) have disappeared, but this degree of resorption is not seen in any other specimen and must be due to decay in an old specimen. Resorption of the plate is not correlated with size for the completely resorbed originals of Pl. 1, figs. 1 and 2 are respectively larger and smaller than Traquair's specimen which is almost perfect.

The vomerine dentition is not well displayed in any of the available specimens,

although some show parts of the supporting bone, but one seems to show remains of the dentition that can be reasonably interpreted (33166, Pl. 2, fig. 4). Watson & Day (1916: 33, text-fig. 6) and others following them showed a pair of elongated plates with three transverse rows of small denticles and a narrow hinder end inserted medially between the front of the entopterygoid tooth-plates. None of the available specimens shows evidence to support this arrangement, which may be based on the uneven resorption of the surface of the entopterygoid tooth-plates, as this tends to start along the mid-line and in front (P. 34543, P. 755, 33166, Pl. 2, figs. 2-4) and the narrow extension of these plates is usually broken away. The last of these specimens shows a very different arrangement: on each vomer there are two or perhaps three

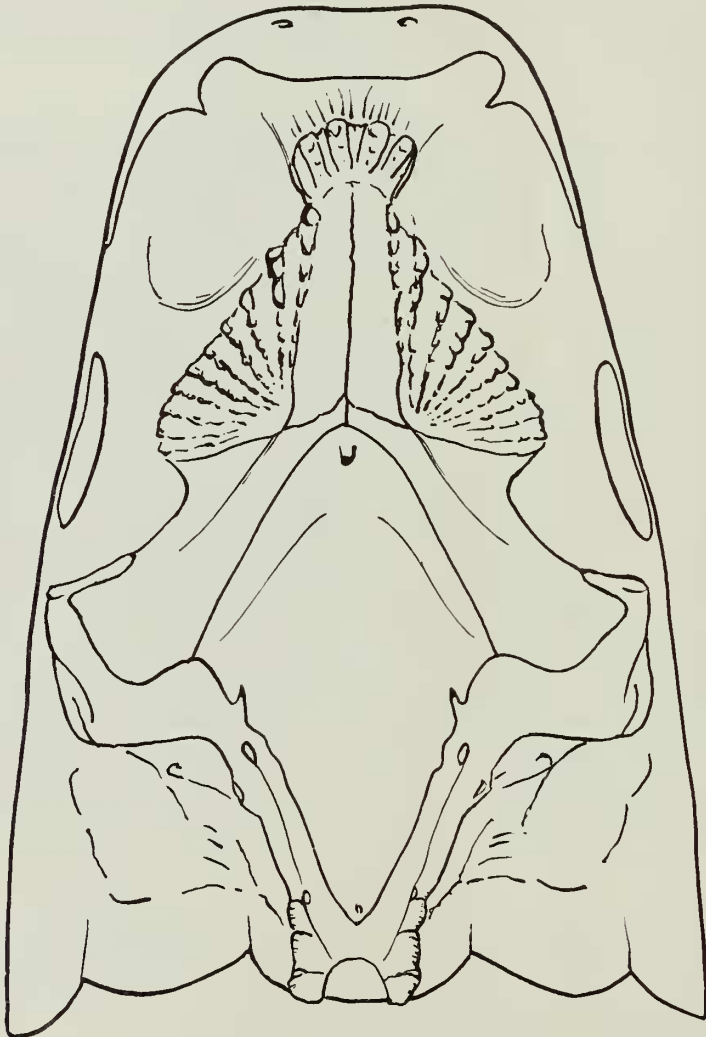


FIG. 50. *Dipterus valenciennesi* S. & M. Restoration of Skull, palatal view.

slightly diverging longitudinal ridges which most probably bore denticles, as Watson noted, although there is little evidence of these now. The vomers are well separated from the hard "lip" and must have bitten against a cartilage pad in the front of the much shorter lower jaw—Günther's (1871: 525, pl. 35, figs. 1-3, *l.a.*) "lower labial cartilage" in *Neoceratodus*—and their function could have been merely to hold before gulping. Günther (1871: 518) refers to the "double kind of action" that the main upper and lower tooth-plates have to perform, crushing or grinding food on the "flat surfaces" and cutting food with the "sharp lateral ridges" which "fit into the notches of the opposite tooth like the shells of a *Cardium*". So very nicely do they fit that there can have been no grinding action involving any degree of lateral displacement, so that the movement must be a simple up and down champing, not quite vertical, for the lower plate is set at a small angle to the horizontal, sloping inwards. And the tooth-plates in *Dipterus*, with their highly denticulated ridges, must have functioned in much the same restricted manner, and such few facets of wear as the denticles show bear this out (P. 34549). Generally speaking the wear is due to friction with the food and just blunts the tubercles which fit into pits of their own making between the radiating rows of denticles on the opposing plate (*e.g.*, 33166, Pl. 2, fig. 4), and in the lower jaw (P. 46692).<sup>1</sup> In old worn dentitions, action was much more irregular and new denticles were sometimes developed between the ridges (P. 34549, Pl. 1, fig. 1).

A restoration of the palatal aspect of *Dipterus* is given in Text-fig. 50.

#### SUMMARY

1. The pattern of the dipnoan skull-roof has developed from an ancestral mosaic principally by loss and invasion of roofing plates; fusion occurs for the most part as an individual aberration.
2. The dipnoi were already widely separated from the Crossopterygii (Jarvik 1960: 32) at their first appearance, and this separation took place when the skull-roof was in a mosaic stage. It is therefore not possible to correlate the plates of the dipnoan skull-roof meaningfully, and attempts to do so must result only in geographical approximations for which compound names have no validity.
3. The use of nomenclature based on that of the skulls of higher vertebrates is therefore both misleading and undesirable: a special notation is required and a modified edition of Forster-Cooper's alphabetical scheme, properly related to the standard sensory canal pattern adequately serves the purpose.

<sup>1</sup> Dr. Gwynne Vevers' observations on the feeding of *Neoceratodus* at the Zoological Gardens in London (*in lit.* 25 Nov. 64) are very much to the point—"We feed the present specimen on strips of raw horse meat or fish approximately  $3 \times \frac{1}{2} \times \frac{3}{8}$  inches. The previous specimens here have all eaten a great deal of lettuce, but the present specimen does not appear to enjoy this at all. . . There is no lateral movement of the jaws in chewing but a very pronounced up and down nibbling movement along the length of the meat strip or fish. The food is then extruded from the mouth and the operation repeated. This may happen several times before the food is finally swallowed. These are straight observations. I suppose the nibbling movement would be a very suitable way of dealing with fresh water crayfish or a similar object."

In a film recently shown by Mr. I. R. Bishop at the Linnean Society of London (20 Feb. 1965) *Lepidosiren* is seen feeding on live worms with exactly the same action as that described above in *Neoceratodus*. *Dipterus* may very well have eaten in a similar fashion once food was obtained, but its heterocercal tail suggests less sluggish movement than in the living lung-fishes and therefore the possibility at times of livelier prey.



4. In the early Dipnoi there was an additional row of plates behind the "extra-scapular" row of *Dipterus* (Z-A-Z) which bore the occipital cross commissure and was later lost.
5. Parallel with the relative movement of the roof-bones in Crossopterygii and higher vertebrates demonstrated by Westoll (1938), there was a movement backwards of the roofing bones of the Dipnoi; while standard plates were developed from the primitive mosaic in front, presumably by loss and invasion, rows of plates were successively lost at the back of the skull-roof, the occipital cross-commissure being in turn captured by the row in front until in Triassic times it was established in Y<sub>1</sub>BY<sub>1</sub>. After the Devonian period there was also an *overall* reduction in the number of the plates, by invasion rather than fusion, a process continued to the present day.
6. The effect of §2 is further to emphasize the difference between the lung-fishes on the one hand and the rhipidistians and coelacanthns on the other. It seems, indeed, on the evidence of the skull-roof patterns that the Dipnoi split off from all the other Osteichthyes at the skull-mosaic stage and developed an independent pattern of dermal bones in the skull-roof which has little relevance to that of the "Teleostomi" in spite of Westoll's ingenious arguments to the contrary and his bold assertion (1949: 159, text-fig. 10) that "The evidence of Devonian forms shows very clearly that the early Dipnoi were very closely related to the contemporaneous Rhipidistia"; my reading of the evidence favours very much Jarvik's (1960: 31-35, text-figs. 28, 30) interpretation of their relationships as an isolated offshoot from "Preteleostomi", and there is a lively expectation that the resemblances that they appear to show towards the contemporary Rhipidistia will prove of decreasing systematic significance. This supposed isolated position is supported by the development of the tooth-plates.
7. In regard to the classification of the Osteichthyes, we are forced back to the ideas of the early years of this century, as expressed by Goodrich (1909) when the first major cleft in the group was placed between the Dipnoi (without, of course, the Arthrodires) and the Teleostomi, equally rated as sub-classes. Lehman (1959: 8) rates the Dipnoi as a Class, but whatever their evaluation, they are an isolated group, and the somewhat heated argument as to the significance of the term "Crossopterygii" and the appropriate label to cover all the Dipnoi Rhipidistia and Coelacanthini (Romer 1955; Trewavas, White, Marshall & Tucker 1955) is so much beating of the air—the Dipnoi stand apart, and the term Crossopterygii covers only the rhipidistians and the coelacanthns.

#### ACKNOWLEDGMENTS

Most of the material studied is in the British Museum (Natural History), and to the collections there substantial and important additions have been made lately by Dr. D. L. Dineley and Mr. John Saxon and his son Alan; and Mr. Saxon has also been able to send valuable information regarding a number of older localities. As usual, ready and patient help with invaluable material on loan from the Royal Scottish Museum was given by Dr. Charles Waterston, and a number of important fossils



from the Manchester Museum were generously lent by Dr. R. M. Eagar. These last were from the D.M.S. Watson collection, and one from Professor Watson's own collection was made available for study as well. Dr. F. R. Parrington also kindly sent me material on loan from Cambridge.

In the Department I had my usual full backing by Mr. Harry Toombs, well supported in the development of the fossil heads by Mr. Ian Macadie, who also influenced the offer of a number of valuable donations from his native Caithness to the right quarter.

The photographs were dexterously taken by Dr. W. T. Dean and Mr. John Ferguson, while in putting the final touches to this document Mr. R. H. Spires, Mr. F. M. Wonnacott and Mr. R. Baker exercised their respective skills.

To all these I offer my sincere thanks.

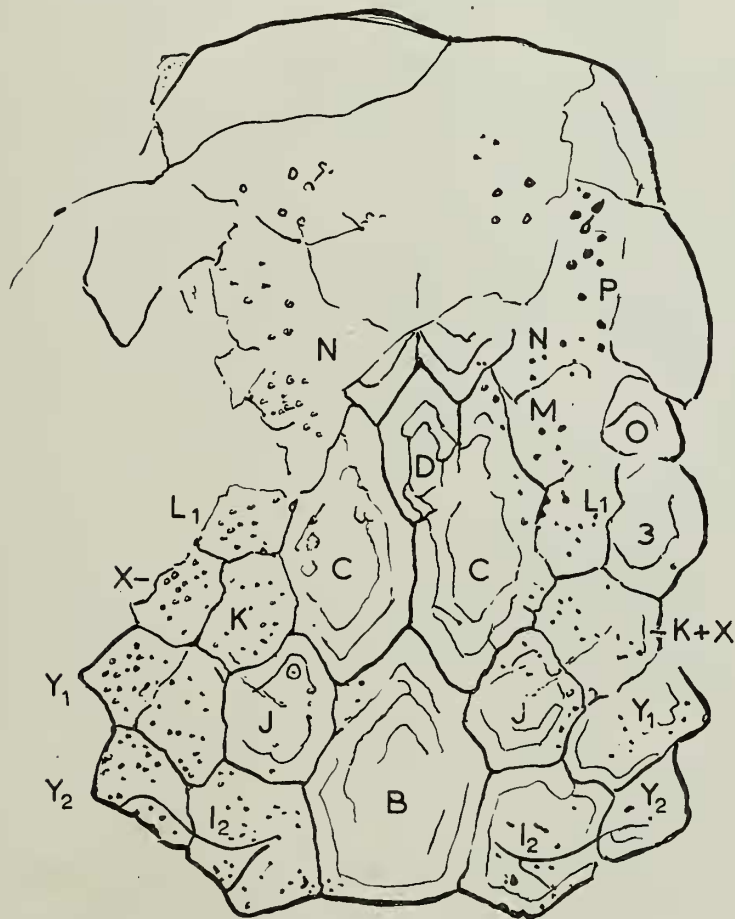


FIG. 51. *Dipterus valenciennesi* S. & M. Skull-roof of small but aged specimen. Lectotype of "*Polyphractus platycephalus*" Agassiz (1844: 5, 29, pl. 27, fig. 1). Orkney. P.3373a.  $\times 1.5$ .

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